

University of Nevada, Reno

Carry-Over Effects and Plumage Polymorphism in Swainson's Hawks

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in
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by

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Abstract

The maintenance of genetic diversity in the face of forces such as genetic drift and natural selection has intrigued scientists for decades. Such processes should seemingly oppose diversity in a stable environment. However, environments are rarely stable in natural systems and processes can be complex. We investigate how a plumage polymorphism is maintained in a population of Swainson's Hawks (*Buteo swainsoni*) in northern California, USA. Swainson's Hawks are highly polymorphic in the belly, flanks and underwing coverts ranging from white to dark brown and seemingly everything in between. Generally, these morphs can be grouped into 3 general classes; light, intermediate and dark.

We first examined potential fitness differences among morph classes. Specifically we examined two primary hypotheses of heterosis (i.e., heterozygote advantage) and apostatic (i.e., frequency dependant) selection. Both mechanisms have been cited before in predator populations as potential mechanisms to maintain a polymorphism. However, we found no evidence of differences in any fitness parameter between the morph classes including; nest success, nest productivity, recruitment of offspring or lifetime reproductive success. There was marginal evidence of differences in survival between morph classes with dark individuals having a slightly higher adult survival compared to intermediate and dark morph.

We also examined sexual selection in this population. Individuals did not appear to mate assortatively (i.e. there was no preference for a mate based on one's own mate class). For females, there was similarly no evidence for imprinting. In contrast, males

chose mates that consistently matched the maternal morph. Further, males selected mates more consistently than we expect by chance. Finally, males that were not able to select mates with the same morph class as their mother had a lower lifetime reproductive success. This result indicates that these males may not have invested as heavily in reproduction, or were lower quality males that could not attract a mate of the correct morph. This sexual selection of the males may aid in the maintenance of the polymorphism over time.

We also examined carry-over effects, processes and events in one season that affect an individual or population in another. Carry-over effects are garnering greater attention in studies of migratory species. Part of this newfound interest stems from tools and techniques allowing researchers to follow individuals or glean greater insights about foraging locations in different times of the year. We used feathers as indices of body condition from both the wintering grounds in Argentina and the breeding area. Specifically, we used the average daily growth of the feather, the level of corticosterone in the feather, and number of fault bars in the retrices and remiges of breeding hawks. We used deuterium levels in feathers to determine where each feather was grown to ensure that indices of condition came from a known location. Average daily growth was correlated with mass adjusted for body size, but corticosterone in feathers and fault bars were not. For males, average daily growth of feathers grown in Argentina and number of fault bars on worn feathers were correlated with nest success demonstrating carry-over effects and that individual in good body condition on their wintering grounds had higher reproductive performance. In contrast, measures of feather condition in females were not correlated with nest success. Corticosterone in feathers was higher in breeding males, but

not in females. As males are the primary providers of prey for both the female and young nestlings their condition may drive the ability of a nesting attempt to succeed because an individual in poor condition may not be able to effectively provision the female or offspring.

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Chapter 1 - Introduction

The evolution of flight and its ability to allow increased movements and migrations and the subsequent variations in plumage that have followed have long fascinated biologists. The advent of powered flight has delivered species into diverse niches and allowed many species to utilize several geographically distinct landscapes, exposing individuals to what could be vastly different environmental conditions and limitations. Biologists are only beginning understand and assess the entire annual cycle with population dynamics of migratory species and plan necessary conservation strategies. Of particular conservation interest, population size and growth may be limited at any of the sites a species uses; breeding areas, wintering areas, or at refueling sites along the migratory route (Sherry and Holmes 1995, Newton 2004, Harrison et al. 2011). Declines in critical resources (e.g. food availability, cover habitat, etc.) in any of these areas can affect the size of a population by changing the carrying capacity. Effects of density dependence will be most profound in the geographic area where resources are most limiting (Sherry and Holmes 1995, Runge and Marra 2005). Therefore, trying to associate population trends of a population with conditions in only one geographic area could provide limited insight or false correlations into factors limiting populations. Recent methodological advances have helped to spark interest in the effects of seasonal interactions on population dynamics observed on the breeding grounds (i.e. carry-over effects, reviewed in Norris 2005, Harrison et al. 2011). Carry-over effects are defined as processes or events in one geographic location that affect an individual or population in another area (Sherry and Holmes 1995, Marra et al. 1998).

Conditions outside of the breeding grounds may affect breeding populations directly (e.g. decreased survival until population is below carrying capacity) or indirectly (e.g. decreased body condition on wintering grounds adversely affecting future breeding). Survival is likely the key population parameter directly limiting population growth in migratory species on the wintering grounds (Newton 2004); however, logistic constraints can limit the ability of researchers to obtain accurate or precise measures of survival while individuals are on the wintering grounds. Also, poor conditions on the wintering grounds may not manifest themselves in an individual until later in the annual cycle. For example, poor conditions on wintering grounds may not appreciably affect over-winter survival. However, poor condition on wintering range may decrease migration survival, as this is when individuals are most energetically challenged. Therefore, using individual body condition as a proxy for future survival may be a reasonable way to determine if and how populations are limited outside of breeding grounds (Norris et al. 2004).

Body condition has already been shown to be a reasonable predictor of survival (Schmutz and Ely 1999), future reproductive performance (Chastel et al. 1995), and overall fitness (Jakob et al. 1996). Body condition may affect an individual's ability to establish and defend territories, avoid predators, provision young, maintain feather condition, etc. Often, body condition is measured using some measure of mass, corrected for the size of the organism (Schulte-Hostedde et al. 2005). By comparing individuals within a population one can determine the average relationship between size and mass, and subsequently judge where individuals are in relation to other individuals in the population. Individuals above the population mean are assumed to be in good body condition and are thought to have extra reserves (e.g. body fat) as a form of energy bank

that can be used in times of stress or low food availability (Jakob et al. 1996). However, other body condition indices have been developed to characterize how well an individual is doing (e.g., Owen 1981, Marra and Holberton 1998). We will use several indices of body condition to examine the population biology of Swainson's Hawks.

The first part of this project will examine seasonal interactions in a population of Swainson's Hawks in Butte Valley, California. Swainson's Hawks are a migratory species that travel to the pampas of Argentina during the nonbreeding season. While in the pampas, Swainson's Hawks can be found in flocks from hundreds to thousands of individuals foraging primarily on grasshoppers and other invertebrates. In the late 1980s through mid-1990s a class of organophosphates, notably monocrotophos and dimethoate, dramatically increased in use to combat large grasshopper swarms (Woodbridge, pers. comm.). These pesticides had dramatic effects on flocks that encountered them, with thousands of individuals found dead as a direct result of pesticide applications (Woodbridge et al. 1995, Goldstein et al. 1996, Goldstein et al. 1999). These pesticides alone may have killed as much as 5% of the global Swainson's Hawk population (Goldstein et al. 1996). However, mortalities to any given breeding population may have been mitigated due to Swainson's Hawks seeming weak migratory connectivity (Sarasola et al. 2008). Despite this weak migratory connectivity, Briggs (2007) found that survival of a population of Swainson's Hawks in northern California had decreased survival in years corresponding to heavy pesticide use, with survival increasing after the pesticides were limited and banned in Argentina. Additionally, reproductive success (i.e. number of fledglings produced per nesting attempt) demonstrated similar declines during years of

heavy pesticide use. While correlative, this evidence is strongly suggestive that poor conditions on the wintering grounds affected population parameters in Butte Valley, CA.

Another aspect of population dynamics that has received a great deal of attention in recent years is the genetic makeup of a population. Molecular work on animal populations has helped provide insight into the immigration rates, prior bottlenecks, and metapopulation dynamics. One area that has garnered substantial attention is the generation and maintenance of genetic diversity, and the subsequent maintenance of phenotypic diversity (e.g. Hoekstra 2006). We know that genetic diversity may help increase a population or species persistence across a landscape. However, multilocus systems require a selective balance to be maintained permanently within a population (Fisher 1930).

One area that has garnered some attention in avian ecology is the rate of melanism within a population. Persistent plumage polymorphisms, or morphs, are color variations within the same age and sex classes (Huxley 1955). These variations are thought to be genetic in most cases, and have been investigated in several species (reviewed in Mundy 2005). In the cases investigated, dark plumage resulted from point mutations of the melanocortin-1 receptor gene (MC1R); these species include Snow Geese (*Anser caerulescens caerulescens*, Mundy et al. 2004), Arctic Skuas (*Stercorarius parasiticus*, Mundy et al. 2004), Red-footed Boobies (*Sula sula*, Baião et al. 2007) and Bananaquits (*Coereba flaveola*, Theron et al. 2001). Polymorphisms are particularly common among raptors, occurring in approximately 33% of species (Galeotti et al. 2003). While a few correlates have been observed between species in the level of polymorphism, few studies have tried to examine intraspecific causes of polymorphism. The second part of this

project proposes to investigate the inheritance and mechanisms for maintaining polymorphisms within our population of Swainson's Hawks in Butte Valley, California.

A number of mechanisms have been used to explain morphs in natural populations. Two of the more common mechanisms are frequency-dependant selection and heterozygote advantage. Frequency dependant selection has been used to explain a number of morphs in populations (Hori 1993, Bond and Kamil 1998, Gigord et al. 2001). Apostatic selection, where the fitness of a phenotype is negatively correlated with its relative frequency within a population, has been used to explain morphs in predator/prey systems (Paulson 1973, Bond and Kamil 1998). In contrast, heterozygous advantage, where heterozygous individuals have an advantage in some fitness component(s) has also been implicated as a mechanism for some systems (Allison 1955, Gulland et al. 1993).

For each of these mechanisms we can predict the direction of fitness for each of the morphs. In apostatic selection, fitness should be highest for the rarest morph type(s), which could lead to changes in morph frequencies over time. However, evidence for this mechanism has been equivocal (Bond and Kamil 1998, Fowlie and Kruger 2003, Galeotti et al. 2003). In contrast, heterosis predicts that in heterozygotes at least some component of fitness should be higher than either homozygous state regardless of frequency in the population.

Despite the differences in predictions in fitness made by the different hypotheses, only a few studies have been able to rigorously examine differences in fitness across the polymorphic gradient within a population. In studies that have examined differences between morphs, it is not uncommon to see differences in life-history strategies or some fitness component. For example, differences in adult survival across morphs have been

described in Tawny Owls (*Strix aluco*, Brommer et al. 2005), Lesser Snow Geese (*Anser caerulescens caerulescens*, Francis et al. 1992), and Common Buzzard (*Buteo buteo*, Krüger et al. 2001b). Alternatively, darker Arctic Skuas (*Stercorarius parasiticus*) bred earlier in the season than lighter individuals when mating for the first time (O'Donald 1983), but lighter individuals, in general, bred at earlier ages than darker birds (O'Donald 1983).

Alternatively, sexual selection may maintain polymorphisms, with hypotheses often centered around assortative mating and imprinting. Assortative mating occurs when individuals select mates of the same or similar phenotypes to themselves (i.e. positive) or of dissimilar phenotypes (i.e. negative). Positive assortative mating based on coloration has been observed in a number of species (Cooke et al. 1976, Abraham et al. 1983, Andersson 1998, Salzburger et al. 2006), and may lead to subsequent genetic divergence between groups (Kirkpatrick 2000). Disassortive mating has similarly been described in a number of species (Throneycroft 1975) and can lead to the maintenance of polymorphisms (Knapton and Falls 1983).

Imprinting on parental phenotypes may also aid the maintenance of polymorphisms. Imprinting on parental phenotypes has been observed in lesser Snow Geese (*Anser c. caenescens*), with individuals having strong preference for parental phenotypes (Cooke et al. 1972, Cooke and McNally 1975). Imprinting has also been cited as a potential mechanism for maintaining polymorphisms when other selective forces are not sufficient to maintain the persistent polymorphism (Krüger et al. 2001a).

The second part of this project will examine potential mechanisms that maintain the polymorphism in our study area. We will take advantage of our long-term dataset to

examine potential differences in fitness across morph classes (e.g, heterosis, apostatic selection) as well as sexual selection in Swainson's Hawks. By examining these differences we can begin to understand the mechanism that maintains this polymorphism and provide information on how genetic diversity in general is maintained.

Literature Cited

- Abraham, K. F., C. D. Ankney, and H. Boyd. 1983. Assortative mating by brant. *The Auk* **100**:201-203.
- Allison, A. C. 1955. Aspects of polymorphism in man. Page 239. Cold Spring Harbor Laboratory Press.
- Andersson, S. 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proceedings of the Royal Society B: Biological Sciences* **265**:445.
- Baião, P. C., F. A. Schreiber, and P. G. Parker. 2007. The genetic basis of the plumage polymorphism in red-footed boobies (*Sula sula*): a Metanocortin-I Receptor (MCIR) analysis. *Journal of Heredity* **98**:287-292.
- Bond, A. B. and A. C. Kamil. 1998. Apostatic selection by blue jays produces balanced polymorphism in virtual prey. *Nature* **395**:594-596.
- Briggs, C. W. 2007. Survival and nesting ecology of Swainson's hawks in Butte Valley, CA. Thesis. University of Nevada, Reno, Reno.
- Brommer, J. E., K. Ahola, and T. Karstinen. 2005. The colour of fitness: plumage coloration and lifetime reproductive success in the tawny owl. *Proceedings of the Royal Society B: Biological Sciences* **272**:935-940.

- Chastel, O., H. Weimerskirch, and P. Jouventin. 1995. Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* **76**:2240-2246.
- Cooke, F., G. H. Finney, and R. F. Rockwell. 1976. Assortative mating in lesser snow geese (*Anser caerulescens*). *Behavior Genetics* **6**:127-140.
- Cooke, F. and C. M. McNally. 1975. Mate selection and colour preferences in lesser snow geese. *Behaviour* **53**:151-170.
- Cooke, F., P. J. Mirsky, and M. B. Seiger. 1972. Color preferences in the lesser snow goose and their possible role in mate selection. *Canadian Journal of Zoology* **50**:529-536.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Fowlie, M. K. and O. Kruger. 2003. The evolution of plumage polymorphism in birds of prey and owls: The apostatic selection hypothesis revisited. *Journal of Evolutionary Biology* **16**:577-583.
- Francis, C. M., M. H. Richards, F. Cooke, and R. F. Rockwell. 1992. Changes in survival rates of lesser snow geese with age and breeding status. *The Auk*:731-747.
- Galeotti, P., D. Rubolini, P. O. Dunn, and M. Fasola. 2003. Colour polymorphism in birds: Causes and functions. *Journal of Evolutionary Biology* **16**:635-646.
- Gigord, L. D. B., M. R. Macnair, and A. Smithson. 2001. Negative frequency-dependent selection maintains a dramatic flower color polymorphism in the rewardless orchid *Dactylorhiza sambucina* (L.) Soo. *Proceedings of the National Academy of Sciences of the United States of America* **98**:6253.
- Goldstein, M. I., T. E. Lacher, Jr., B. Woodbridge, M. J. Bechard, S. B. Canavelli, M. E. Zaccagnini, G. P. Cobb, E. J. Scollon, R. Tribolet, and M. J. Hooper. 1999.

- Monocrotophos-induced mass mortality of Swainson's hawks in Argentina, 1995-96. *Ecotoxicology* **8**:201-214.
- Goldstein, M. I., B. Woodbridge, M. E. Zaccagnini, S. B. Canavelli, and A. Lanusse. 1996. An assessment of mortality of Swainson's hawks on wintering grounds in Argentina. *Journal of Raptor Research* **30**:106-107.
- Gulland, F. M. D., S. D. Albon, J. M. Pemberton, P. R. Moorcroft, and T. H. Clutton-Brock. 1993. Parasite-associated polymorphism in a cyclic ungulate population. *Proceedings: Biological Sciences* **254**:7-13.
- Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* **80**:4-18.
- Hori, M. 1993. Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. *Science* **260**:216.
- Huxley, J. 1955. Morphism and evolution. *Heredity* **9**:1-53.
- Jakob, E. M., S. D. Marshall, and G. W. Uetz. 1996. Estimating fitness: A comparison of body condition indices. *Oikos* **77**:61-67.
- Kirkpatrick, M. 2000. Reinforcement and divergence under assortative mating. *Proceedings of the Royal Society B: Biological Sciences* **267**:1649-1655.
- Knapton, R. W. and J. B. Falls. 1983. Differences in parental contribution among pair types in the polymorphic white-throated sparrow. *Canadian Journal of Zoology* **61**:1288-1292.
- Krüger, O., J. Lindstrom, and W. Amos. 2001a. Maladaptive mate choice maintained by heterozygote advantage. *Evolution* **55**:1207-1214.

- Krüger, O., J. Lindström, and W. Amos. 2001b. Maladaptive mate choice maintained by heterozygote advantage. *Evolution* **55**:1207-1214.
- Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science (Washington D C)* **282**:1884-1886.
- Marra, P. P. and R. L. Holberton. 1998. Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. *Oecologia* **116**:284-292.
- Mundy, N. I. 2005. A window on the genetics of evolution: MC1R and plumage colouration in birds. *Proceedings of the Royal Society Biological Sciences Series B* **272**:1633-1640.
- Mundy, N. I., N. S. Badcock, T. Hart, K. Scribner, K. Janssen, and N. J. Nadeau. 2004. Conserved genetic basis of a quantitative plumage trait involved in mate choice. *Science (Washington D C)* **303**:1870-1873.
- Newton, I. 2004. Population limitation in migrants. *Ibis* **146**:197-226.
- Norris, D. R. 2005. Carry-over effects and habitat quality in migratory populations. *Oikos* **109**:178-186.
- O'Donald, P. 1983. *The Arctic skua: A study of the ecology and evolution of a seabird.* Cambridge University Press, Cambridge (UK).
- Owen, M. 1981. Abdominal profile: a condition index for wild geese in the field. *The Journal of wildlife management* **45**:227-230.
- Paulson, D. R. 1973. Predator polymorphism and apostatic selection. *Evolution*:269-277.

- Runge, M. C. and P. P. Marra. 2005. Modelling seasonal interactions in the population dynamics of migratory birds. Pages 375-389 in R. Greenberg and P. P. Marra, editors. *Birds of two worlds: the ecology and evolution of the temperate-tropical migration systems*. Johns Hopkins University Press, Baltimore, MD.
- Salzburger, W., H. Niederstätter, A. Brandstätter, B. Berger, W. Parson, J. Snoeks, and C. Sturmbauer. 2006. Colour-assortative mating among populations of *Tropheus moorii*, a cichlid fish from Lake Tanganyika, East Africa. *Proceedings of the Royal Society B: Biological Sciences* **273**:257-266.
- Sarasola, J. H., J. J. Negro, K. A. Hobson, G. R. Bortolotti, and K. L. Bildstein. 2008. Can a 'wintering area effect' explain population status of Swainson's hawks? A stable isotope approach. *Diversity and Distributions* **14**:686-691.
- Schmutz, J. A. and C. R. Ely. 1999. Survival of greater white-fronted geese: effects of year, season, sex, and body condition. *Journal of Wildlife Management* **63**:1239-1249.
- Schulte-Hostedde, A. I., B. Zinner, J. S. Millar, and G. J. Hickling. 2005. Restitution of mass-size residuals: Validating body condition indices. *Ecology* **86**:155-163.
- Sherry, T. W. and R. T. Holmes. 1995. Summer versus winter limitation of populations: conceptual issues and evidence. Pages 85-120 in T. E. Martin and D. M. Finch, editors. *Ecology and management of neotropical migratory birds. A synthesis and review of critical issues*. Oxford University Press, New York.
- Theron, E., K. Hawkins, E. Bermingham, R. E. Ricklefs, and N. I. Mundy. 2001. The molecular basis of an avian plumage polymorphism in the wild: A melanocortin-

1-receptor point mutation is perfectly associated with the melanic plumage morph of the bananaquit, *Coereba flaveola*. *Current Biology* **11**:550-557.

Throneycroft, H. B. 1975. A cytogenetic study of the white-throated sparrow, *Zonotrichia albicollis* (Gmelin). *Evolution* **29**:611-621.

Woodbridge, B., K. K. Finley, and S. T. Seager. 1995. An investigation of the Swainson's hawk in Argentina. *Journal of Raptor Research* **29**:202-204.

Chapter 2 - Plumage polymorphisms and fitness in Swainson's hawks

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Abstract

We examine the maintenance of a plumage polymorphism, variation in plumages among the same age and sex class within a population, in a population of Swainson's Hawks.

We take advantage of 32 years of data to examine 2 prevalent hypotheses used to explain the persistence of morphs; apostatic selection and heterozygous advantage. We

investigate differences in fitness among three morph classes of a melanistic trait in

Swainson's Hawks: light (7% of the local breeding population), intermediate (57%) and dark (36%). Specifically, we examined morph differences in adult apparent survival,

breeding success, annual number of fledglings produced, probability of offspring

recruitment into the breeding population, and lifetime reproductive success. If apostatic

selection were a factor in maintaining morphs we would expect that individuals with the least frequent morph would perform best in one or more of these fitness categories.

Alternatively, if heterozygous advantage played a role in the maintenance of this

polymorphism we would expect heterozygotes (i.e. intermediate morphs) to have one or

more increased rates in these categories. We found no difference in adult apparent

survival between morph classes. Similarly, there were no differences in breeding

success, nest productivity, lifetime reproductive success or probability of recruitment of

offspring between parental morph. We conclude that neither apostatic selection nor

heterozygous advantage appear to play a role in maintaining morphs in this population.

Keywords: apostatic selection, *Buteo swainsoni*, heterozygous advantage, lifetime

reproductive success, melanin, recruitment, survival

Introduction

Plumage color polymorphisms (hereafter morphs), differences in plumage color in the same age and sex class within a population, have been the subject of a number of studies investigating the maintenance of genetic diversity (e.g., Baiao & Parker, 2008, Brommer et al., 2005, Comendant et al., 2003). Often morphs appear to be genetically determined (Mundy, 2005, Hoekstra, 2006), and how these genes are maintained in the face of selection and genetic drift may help illuminate other studies of genetic diversity. A number of mechanisms have been used to explain morphs in natural populations, and often these mechanisms are linked to relative fitness of different morph types (Meunier et al., 2011). Some of the more common mechanisms are frequency-dependant selection, heterozygote advantage, genotype-by-environment interactions and local adaptation. Frequency dependant selection has been used to explain plumage polymorphisms in a number of species (Hori, 1993, Bond & Kamil, 1998, Gigord et al., 2001). Apostatic selection, where the fitness of a phenotype is negatively correlated with its relative frequency within a population, has been used to explain morphs in predator/prey systems (Bond & Kamil, 1998, Paulson, 1973). In contrast, heterozygous advantage, where heterozygous individuals have an advantage in some fitness component(s) has also been implicated as a mechanism for some systems (Allison, 1955, Gulland et al., 1993). Heterozygote advantage, or heterosis, has been proposed as a way to mask deleterious alleles and can be generally beneficial in a number of species (Brown, 1997, Mitton, 1993).

For each of these mechanisms we can predict the direction of fitness for each of the morphs. In apostatic selection, fitness should be highest for the rarest morph type(s),

which could lead to changes in morph frequencies over time. Specifically, at the equilibrium frequency the fitness of morphs should be equal. Thus, the rare morph will only have increased fitness up to some equilibrium point. However, evidence for this mechanism has been equivocal (Fowlie & Kruger, 2003, Galeotti et al., 2003, Bond & Kamil, 1998). In contrast, heterosis predicts that in heterozygotes at least some component of fitness should be higher than either homozygous state regardless of frequency in the population.

Despite the differences in predictions in fitness made by the different hypotheses, only a few studies have been able to rigorously examine differences in fitness across the polymorphic gradient within a population. In studies that have examined differences between morphs, it is not uncommon to see differences in life-history strategies or some fitness component (Roulin, 2004). For example, differences in adult survival across morphs have been described in tawny owls (*Strix aluco*, Brommer et al., 2005), lesser snow geese (*Anser caerulescens caerulescens*, Francis et al., 1992), and common buzzards (*Buteo buteo*, Krüger et al., 2001b). However, in lesser snow geese any potential advantage does not translate into increased fitness between the morph classes (Cooke & Davies, 1983). Alternatively, darker Arctic skuas (*Stercorarius parasiticus*) bred earlier in the season than lighter individuals when mating for the first time (O'Donald, 1983), but lighter individuals, in general, bred at earlier ages than darker birds (O'Donald, 1983).

In predatory species, there is evidence of each mechanism maintaining polymorphisms. For example, in arctic skuas, there was evidence of apostatic selection in kleptoparasitism rates (Arcos, 2007, Caldow & Furness, 1991). There is additional

evidence in a comparative study of raptors that polymorphic species prey on more mammals more frequently than monomorphic species (Roulin & Wink, 2004). In contrast, studies of the common buzzard have demonstrated a potential heterozygote advantage for a population in western Germany (Krüger et al., 2001b). In that population intermediate individuals had higher survival, reproduction, reproductive value, and lifetime reproductive success (LRS, Krüger et al., 2001b, Chakarov et al., 2008) which helped maintain the polymorphism in the population. Thus, maintenance of polymorphisms in other *Buteo* species may be related to heterosis

Plumage polymorphisms may also be maintained by genotype-by-environment (GE) interactions, wherein some morph types are selectively favored in certain habitat types (Levene, 1953, Levins & MacArthur, 1966, Hedrick et al., 1976). In species with high dispersal distances or a large amount of gene flow polymorphisms may be maintained by mixing of morphs between habitats. This mixing would effectively prevent any population from being completely matched with the appropriate habitat phenotype (Räsänen & Hendry, 2008, Postma & van Noordwijk, 2005, Antoniazza et al., 2010). If GE interactions played a role in the maintenance of a polymorphism the most dominant allele should have the highest fitness (Antoniazza et al., 2010). In barn owls (*Tyto alba*), individuals may be adapted for a specific habitat types. Mixing of individual adapted to different habitat types likely prevents local adaptation of all individuals within an area (Antoniazza et al., 2010). Further, differential habitat selection has been observed between morphs of red-tailed hawks (*Buteo jamaicensis*, Preston, 1980).

Alternatively, there may not be selective advantages or differences in life-history strategies that maintain different morphs within a population. Factors such as sexual

selection (e.g., assortative mating, see review in Lank, 2002) or large population size (Fowlie & Kruger, 2003) may maintain multiple morphs within a population not requiring further explanations of fitness differences. Indeed, a number of studies have not found differences in components of fitness among morphs within populations (reviewed in Meunier et al., 2011). However, to better understand what mechanisms may maintain polymorphisms within a population, it is necessary to first examine if there are differences in vital rates and subsequent potential fitness differences within a population.

Swainson's hawks (*Buteo swainsoni*) are known for an almost continuous plumage variation from light to dark in the underwing coverts, axillaries and belly (England et al., 1997, Palmer, 1988), particularly on the western edge of their range (Wheeler, 2003, Sharp, 1902). This variation is generally divided into three categories; light, intermediate/rufous and dark (Wheeler, 2003, Palmer, 1988). These categories follow a one-locus two-allele pattern where light and dark morph individuals are homozygous and intermediate/rufous individuals are heterozygous (Briggs et al., 2010a) and morph does not change over the course of an individual's lifetime (Briggs et al., 2010b). The heritability of these plumage categories seem generalizable across the genus *Buteo* and has been found in both Common Buzzards (Krüger et al., 2001b) and Ferruginous Hawks (*Buteo regalis*, Schmutz & Schmutz, 1981). Swainson's hawks, like several *Buteo* species in North America, exhibit a strong east to west cline in plumage melanization, with a higher proportion of dark morphs on the western end of their breeding range (Wheeler, 2003).

We take advantage of a 32-year study of Swainson's hawks to investigate differences in several aspects of fitness among morph classes of Swainson's hawks.

Specifically, we investigate differences among morphs in adult survival, reproductive rates, lifetime reproductive success and offspring recruitment. If heterosis is helping to maintain morphs, we would expect intermediate individuals to have increased values in one or more of the demographic population parameters. Alternatively, if apostatic selection is maintaining morphs in the population we would expect one or more vital rates to be negatively correlated with their relative frequency in the population. We also may expect one or more vital rates to change over time in varying manners (e.g., light morph reproduction to increase as dark morph reproduction decreases over years as prey species associate different morph types with danger). By investigating these hypotheses we hope to elucidate the mechanism(s) maintaining morphs in Swainson's hawks.

Materials and methods

We conducted our study in the Butte Valley, California (49° 41' N, 122° 00' W) from 1979 to 2010. The study area is approximately 400 km² valley in the Great Basin ecoregion (Franklin & Dyrness, 1973). Adult hawks were captured using bal-chatri traps baited with mice or a dho-gaza style net with a great-horned owl (*Bubo virginianus*) lure near nest sites (Bloom et al., 1992). Hawks captured were given a 2-digit alphanumeric color band for individual identification in addition to a US Geological Survey (USGS) aluminum band, unless they were already banded with a USGS aluminum band. Adults were photographed opportunistically in the hand over the course of the study to document morph. Nest sites were located by watching for nest building, territorial behavior, and copulations early in the season (Apr – May), and prey deliveries late in the season (May - Aug). Nestlings were banded with USGS aluminum bands ~1-2 weeks prior to fledging. Adults observed nest building, delivering prey, or actively defending the area

immediately around the nest site were considered the parents of any nestlings. Extra-pair copulations (EPCs) have been observed in the population (BW, pers obs), but we were unable to document the frequency of EPCs or extra-pair paternity in this population.

Individuals were placed into categories of light, intermediate and dark morphs based on amount of melanism in the belly, flanks and underwing coverts (Briggs et al., 2010b). Individuals were considered light if they had no visible melanistic plumage in their belly underneath the bib, flanks or underwing coverts. Intermediate morphs had some melanistic plumage in their belly and flanks, although not always in their underwing coverts. Melanistic plumage of intermediate morphs never entirely covered the area under the bib, allowing the observer to distinguish the bib. The bib in dark morph individuals was indistinguishable from the belly or flanks due to extensive pigmentation across those areas. Additionally, there was always some pigmentation in the underwing coverts. All procedures were approved by the Institutional Animal Care and Use Committee at the University of Nevada, Reno (IACUC approval no. 00115).

We first looked for differences in morph frequencies between males and females using a chi-square analysis, using all individuals marked and classified as a breeder throughout the course of the study. We also used a principal components analysis to obtain a single size variable based on length of wing chord and tail measures. We used the first principal component as a surrogate for size (Pimentel, 1979), which explained 89% of the variation in the data. To determine if there were size differences across morph classes we regressed size against morph and sex in both additive and interactive models using a linear model (LM) with a normal distribution. We also examined differences in body condition among morph classes. Specifically, we regressed weight

against body size using a LM. We then regressed the residuals of the previous LM against morph, sex, day of breeding season an individual was trapped, and all interactions.

Adult Apparent Survival

We used multistate models in Program MARK (White & Burnham, 1999) to examine differences in survival of different morph classes from individuals trapped, marked and observed between 1979-2010. Multistate models were necessary to account for loss of color bands, and therefore differential encounter probability between individuals with and without a color band. Thus, we estimated four parameters: apparent survival (Φ), encounter probability (p), transition probability from color banded to non-color banded (ψ_{CB-NCB}), and transition probability from non-color banded back to color banded (ψ_{NCB-CB}). ψ was estimated using an MLogit link to ensure that probabilities of ψ_{NCB-CB} and ψ_{CB-NCB} summed to 1.0. As ψ and p were considered nuisance parameters, we first modeled these to obtain the best model fit. We modeled ψ using band age and relative trapping effort. We used relative survey effort and morph class to model p to account for potential differences in detectability between morphs as well as strata. Survey effort was rated as high, moderate or low, depending on the number and experience of field technicians working in a given year. We modeled Φ using a quadratic temporal trend described previously (Briggs, 2007). We grouped individuals into light, intermediate and dark morphs using pictures of individuals taken when they were trapped or when they were soaring. Individuals were independently assigned by two observers into classifications (Briggs et al. 2010a). We modeled morph classes as groups,

examining differences in apparent adult survival between morphs across time. We used Program U-Care to examine the underlying assumptions of the multistate model to determine if there could be overdispersion in the data and correcting for potential overdispersion using \hat{c} (Choquet et al., 2009, Choquet et al., 2005), however there was no evidence of overdispersion with all tests from U-Care (i.e. tests 3.SR, 2.CT, 3G.SR, M.ITEC, and M.LTEC; $P > 0.28$ for all tests).

We used Akaike's Information Criterion (AIC, Akaike, 1973) adjusted for small sample sizes and overdispersion (i.e., QAIC_c) to rate candidate models and create model weights representing the relative likelihood of each candidate model (Burnham & Anderson, 2002). We calculated model weights to provide an index of likelihood for each candidate model (Burnham & Anderson 2002); models with the lowest QAIC_c were considered to have more support. The relative strength for each model term (e.g., sex) can be assessed by summing the weights of all models containing a particular term ($\sum \omega_i$), with greater model weights indicating greater support for a model. Model weights were then used to calculate mode-averaged parameter estimates (Burnham & Anderson, 2002).

Reproduction

We examined reproduction through analysis of both nest survival and nest productivity. Nest survival was defined by whether a nest failed (i.e., produced no fledglings) or succeeded (i.e., produced at least one fledgling). We quantified nest survival using hierarchical Bayesian daily nest survival models (Schmidt et al., 2010) that calculated potential differences between both maternal and paternal morph classes in nest survival using the R package "R2WinBUGS" (Sturtz et al., 2005) in R 2.10.1 and

WinBUGS 1.4.3 (Lunn et al., 2000). These models account for biases in apparent nest survival, due to a potential to miss nests after they have failed, by accounting for nest detection probability (Mayfield, 1961, Mayfield, 1975). They also account for potential problems with pseudoreplication of monitoring the same nest sites over multiple years (Hurlbert, 1984). Using these models, we examined the influence of morph of the attendant male and female on nest survival. We also examined the putative offspring morph ratio of light, intermediate and dark individuals (Briggs et al., 2010a). If heterozygous advantage aided nestling survival, we would expect higher nest survival of nests with higher proportions of heterozygous chicks. However, because morph of offspring was not generally recorded over the course of the study, we were forced to use expected morph ratio based on a simple one-locus, two allele inheritance pattern observed in Swainson's hawks (Briggs et al., 2010a). Finally, we used the proportion of each of the adult morphs in the population, expecting a negative correlation with nest survival if apostatic selection were occurring. However, since we did not have information for most years of the study to adequately calculate daily nest survival, we limited the dataset to years when we had adequate data. Convergence of the Markov chain Monte Carlo (MCMC) runs was assessed using the Rafert-Lewis and Gelman-Rubin diagnostic tests in the R package "coda" (Plummer et al., 2006, Gelman & Rubin, 1992). We used a reversible jump Monte Chain Monte Carlo (RJMCMC) method through the WinBUGS JUMP interface (Lunn et al., 2009, Spiegelhalter et al., 2002). RJMCMC was used to assess the performance of covariates using the posterior probability (Green, 1995), and covariates with a high marginal posterior probability (i.e., >0.85) were considered influential. We used flat, or uninformative, priors so that each

model had an equal likelihood *a priori*, with 150,000 iterations, discarding the first 15,000 as burn-in to ensure complete mixing. A RJMCMC allows the model to move through parameter space, selecting covariates if they aid in model fit. At each step of the MCMC the parameter values in the model are updated. Thus, for each step we can determine parameter values and which parameters have been selected. At the end of the modeling, the amount of time spent in a given model (i.e. the marginal posterior probability) indicates the relative support for that model. Cumulative statistics of parameters of interest (e.g., mode, credible intervals) can then be extracted using MCMC that account for model uncertainty (King & Brooks, 2004). Data on nest initiation as well as on nest checks are necessary for this modeling procedure, and adequate data were only available from 1993, 1995, and 2008-2010 when nests were checked frequently enough to estimate daily nest survival rates.

To examine nest productivity we used a mixed-effects regression using package lme4 (Bates & Maechler, 2009) in R 2.10.1 (R Development Core Team, 2009) with a Poisson distribution, a log-link and a Laplace approximation (Bolker et al., 2009), for all successful nests where the morph of both parents was known from 1979-2010. We could use an expanded dataset because we were not restricted to years when there were frequent nest visits to assess nest activity. We regressed number of fledglings against morph of attendant adults. We also used putative offspring morph ratio as a covariate to determine if offspring production was related to likely offspring morphs and annual frequency of the adult morph in the population as covariates in our regression. Because we were not restricted to nests where nest-initiation date was known, we could take advantage of all known successful nests from 1979-2010 with attendant parents with at least one known

morph. Nestlings were considered fledged once they reached 80% of fledgling age (Steenhof, 1987).

Lifetime Reproductive Success and Recruitment

We used a generalized linear model with a quasiPoisson distribution (Hoef & Boveng, 2007) in R 2.10.1 to determine if there were differences in LRS across morph classes. We also used the year an individual was observed first breeding and the interaction between year and morph to investigate temporal patterns in LRS. We used a quasiPoisson distribution to account for overdispersion of the data (i.e. a variance greater than the mean). To account for detection rates that were less than 100% and avoid any bias in our estimates of LRS, we censored individuals if we knew they were missed for >2 years (i.e. there were >2years the individual was not observed in between years when they were observed). We chose two years because only missing an individual for two years could mean that the individual merely failed in those seasons and was subsequently not available to be encountered if it left the study area. Additionally, even if an individual bred successfully in both years we did not detect it, those years would be unlikely to cause significant bias in our results because mean individual lifespan of breeding individuals is >8 years (Briggs et al., in press).

To determine offspring probability of recruitment we used a logistic regression mixed-model using the lme4 package in R 2.10.1. Parental male and female morphs were used as groups to examine differences in offspring recruitment between different morph adults. We also used the individual's relative morph proportion in the population in our regression of offspring recruitment probability. For models of nest productivity,

LRS and recruitment, we used AIC_c to assess relative model fit to the data. As in the apparent survival analysis, we used the sums of the model weights and model averaging to determine the relationship between covariates and each of the described variables.

Morph frequencies over time

We examined changes in frequencies of morphs over the course of the study by grouping all individuals observed within 5yr blocks and using a chi-square analysis to determine if there were differences between blocks.

Results

From 1979-2010, we banded 1389 nestlings and 337 breeding Swainson's hawks. Of the 337 breeders, 124 were initially banded as nestlings in the population and 249 were photographically documented. In the population as a whole there were no differences between the morph distribution of males and females ($\chi^2=0.445$, $P=0.80$; Fig. 1). There also were no size differences between different morph classes for either males ($n=57$) or females ($n=47$) based on the first principal component of size, using tail length and wing chord ($P>0.15$ for all comparisons). Similarly, there were no differences in body condition between morph classes (light, $n=4$; intermediate, $n=60$; dark, $n=30$; $df=93$; $P>0.22$ for all comparisons).

Adult Apparent Survival

We banded and monitored 17 light, 143 intermediate, and 89 dark morph individuals as adults during the 32-year study. We observed an average of 44.1 ± 4.2 (mean \pm SE) marked adults per year. There was no difference in probability of detection (p) among morph classes, and p varied between states and by survey effort. ψ_{CB-NCB} was

higher in the first year after capture (0.14 ± 0.02) than in subsequent years (0.08 ± 0.02). Ψ_{NCB-CB} (0.26 ± 0.03) was unrelated to age of the color band or sex of the individual. There was considerable evidence of differential survival across morphs in a quadratic temporal trend ($\Sigma\omega_i=0.99$; Table 1). Model-averaged survival of dark individuals was higher than light or intermediate morph individuals during the mid-1990s (Fig. 2); however, 95% confidence intervals were overlapping for all differences between morph classes (Table 2). Tests of assumptions of the underlying model suggest that there were no problems with overdispersion of the data ($P > 0.28$ for all tests; $\hat{c}=0.86$).

Reproduction

We observed 123 nest attempts with a known male, 108 where the female was known, and 78 where both morphs were known in 1993, 1995, and 2008-2010 (i.e. years when data were adequate to examine daily nest survival). There was no correlation between parental morph, likely offspring morph ratio (i.e., the morph ratio of offspring expected given a Mendelian inheritance pattern), or parental morph frequency in the population (Table 3). The highest marginal probability from the Bayesian analysis for any morph group was 0.13 for females, and 0.54 for males, indicating low support (i.e. < 0.85 marginal posterior probability) for any covariate.

We modeled nest productivity for 200 successful nesting attempts from 1985 – 2010, where both parents had known morphs. Average number of young fledged from those nests was 2.1 ± 0.1 . There was limited evidence that number of fledglings declined over the course of the study, though the parameter estimate significantly overlapped 0 ($\beta = -0.03 \pm 0.05$; $\Sigma\omega_i=0.23$; Table 4). There was no correlation between the number of

offspring produced and morph of either parent, likely offspring morph ratio, parental morph frequency in the population, or interactions with any of those variables and temporal trends over the course of the study (Table 4).

Lifetime Reproductive Success and Recruitment

We banded and monitored 12 light (6 male, 6 female), 74 intermediate (41 male, 33 female) and 51 dark morph (26 male, 25 female) individuals who met the requirements to be included in the analysis of LRS. There was no morph difference between the individuals used in the analysis and those that were censored because they were missed >2 times over the course of the study ($\chi^2=3.23$, $P=0.20$). Average LRS for males was 6.4 ± 0.8 and for females was 6.5 ± 0.8 . There were no differences in LRS between any of the morph groups for males or females ($\Sigma\omega_i < 0.01$; Table 5; Fig. 3).

Similarly, there were no differences in probability of recruitment of offspring of the different morph classes for males ($\Sigma\omega_i=0.07$) or females ($\Sigma\omega_i=0.05$), or the probable morph proportions of offspring (Table 6). There also was no evidence that an individual's proportion of morph was related to number of offspring fledged for males ($\Sigma\omega_i=0.22$) or females ($\Sigma\omega_i=0.09$). We banded 257 offspring from pairings where both parents had known morphs, of which 36 recruited into the population. Morph was recorded for 28 of those recruited offspring, and the proportion of those individuals was not significantly different than what would be expected based on known inheritance patterns (Briggs et al. 2010a) and parental morph of those individuals ($\chi^2=3.62$, $P=0.16$).

Morph frequencies over time

We observed a total of 258 individuals in Butte Valley with known morph between 1979-2010. There was no variation among morph frequencies between any of the 5 year periods ($\chi^2=12.03$, $P=0.28$, Fig. 4).

Discussion

Heterosis

We found no evidence that intermediate individuals had increased levels of any component of fitness examined. In reproduction, heterosis could benefit one or both heterozygote parents through increased nest survival, number of offspring fledged or increased recruitment rates. Alternatively increases in the number of heterozygous offspring could increase fitness. However, we did not find evidence for either of these predictions. Without any increases in population parameters it seems unlikely that heterosis could maintain morphs in this population. Predicted number of heterozygous offspring based on Mendelian inheritance was not a reasonable predictor of nest success. However, these were estimates of heterozygous offspring based on the Mendelian pattern observed in this population (Briggs et al., 2010a), and future work should examine the realized offspring morphs relative to reproduction and offspring recruitment.

Our study contrasts several studies of common buzzards in Germany that recorded advantages in reproduction and survival of heterozygous morphs, suggesting that heterosis was helping to maintain the plumage polymorphism in that population (Chakarov et al., 2008, Krüger et al., 2001a). Our study was able to more rigorously examine correlates of fitness, due to banding and our ability to intensively track

individuals over a long time period. We also were able to examine not only adult apparent survival, nest survival, offspring production and LRS, but we were able to examine differential recruitment of offspring, which may provide a better index of fitness than measures used by others (e.g., Newton, 1989).

Apostatic Selection

Similarly, there was no evidence that apostatic selection plays a role in maintaining multiple morphs in this population. If prey could differentiate predator morph and react differentially to the least common morph, we would expect light morphs to have higher vital rates in this population, and that proportions of morphs should oscillate over generational time. A lack of significant differences in morph frequencies over the course of the study (Figure 4) indicates a lack of directional selective pressure or fitness differences in this population and may indicate that morph is selectively neutral in this population. There were no significant differences among blocks of years, with the least common morph (i.e. light morphs) not increasing significantly over the course of the study.

If the rarest morphs had a greater ability to catch prey or expended less effort in catching prey, we would expect to see differences in reproduction, as long-lived species should favor survival in the face of a trade-off between survival and reproduction (Stearns, 1992). However, there was no evidence of increased reproduction in light morphs. Even if apostatic selection changed reproductive success at rates too subtle for us to detect (i.e. within 95% confidence interval) or at a temporal scale we did not measure, we would expect morph frequencies to change over generational time due to

fluctuating recruitment of relatively lighter or darker individuals. However, morph frequencies have not changed in our study area in the last 25 years. The lack of changing morph frequencies over time, coupled with these results strongly suggest a lack of apostatic selection in this population, contrary to results reported in another Swainson's hawk population (Arcese and Fitzner 1982). This study, however, had relatively low sample sizes and could not differentiate between heterosis and apostatic selection.

Although Belding's ground squirrels (*Spermophilus beldingi*), the primary prey in this study area (Woodbridge, 1991), seem to differentiate flying raptors from other birds in flight (Robinson, 1980), the closely-related California ground squirrel (*Spermophilus beecheyi*) reacts with fear to novel stimuli (Hanson & Coss, 1997). Therefore for rodent species that are frequently preyed upon by raptors, the natural reaction may be to fear novel stimuli and only acclimate to those species that do not pose a threat, providing little opportunity for apostatic selection.

GE Interactions

Dark morph adult apparent survival was higher than light or intermediate morph survival, though confidence intervals for the measures overlapped between all morph categories. This result suggests a GE interaction, where the most common allele in the population (i.e. for dark individuals) may be better adapted for the study area. Further, the lack of population structure for Swainson's Hawks in the Great Plains and Great Basin (Hull et al., 2008) suggests that this polymorphism may in fact be maintained by gene flow from eastern areas of the species range, where light morphs are dominant (Wheeler, 2003) and could have a selective advantage. The cause of this apparent

increase in survival is unknown, but could be related to a number of factors, such as reduced parasite loads due to melanic plumages (Goldstein et al., 2004), pleiotropy (Ducrest et al., 2008) or thermal physiology (Mosher & Henny, 1976, Ward et al., 2007). A similar selective advantage for darker individuals was reported in barn owl females (Roulin et al., 2010) and is likely related to environmental variation (Roulin et al., 2009). The sex-dependant selection led to increased melanization in that population over the course of a 12-year period (Roulin et al., 2010). We could not rule out the possibility that morphs are adapted to alternative habitats, as is found in barn owls (Antoniazza et al., 2010) and that such an adaptation may lead to dark morphs having slightly increased survival. Alternatively, differing environmental conditions could favor morphs. Thus we might expect that climactic conditions (e.g., rainfall) could cause variation in selective pressure over time, resulting in a lack of differences in fitness components across morph categories.

Despite the apparent survival advantage of dark morphs, and a lack of differences in reproduction between morph classes, there were no differences in LRS between morphs, suggesting there was no overall fitness advantage for different morph classes at the scale we were able to measure. In fact, both light and intermediate morph classes had individuals with higher LRS than dark morph individuals, despite potential increased opportunity for reproduction. While we may have limited ability to detect differences in LRS across groups (e.g., due to difficulty detecting individuals when they initially are recruited into the breeding population), it seems that the slight survival advantage observed in this population is not enough to drive fitness differences at the level we can observe. However, if the survival advantage is real and our measure of LRS is too

imprecise to find a difference, then such fitness differences may drive the population out of Hardy-Weinberg equilibrium that we observe (C.W.B., unpub. data), and maintain the cline in morph observed in the populations breeding range (Wheeler, 2003).

Despite our ability to assess measures of fitness in adults, we could not assess if any of the proposed mechanisms were factors in juvenile and subadult survival. While it appears there are no differences in nestling survival based on the proportion of morphs we would expect in a given nest attempt, we did not know the morph of nestlings for the analysis. Therefore, we were forced to use the expected morph frequencies of nestlings, which is likely only a crude representation and have the potential to obscure any relationship between offspring morph and nest or nestling survival. However, the recruits that returned as breeders that had known parents were not significantly different than we would expect based on the reported one-locus, two-allele genetic system that seem to control morph in Swainson's hawks (Briggs et al., 2010a).

While we did not find a selection mechanism for maintaining morphs, they could be maintained in the face of genetic drift if the population is sufficiently large (Fowlie & Kruger, 2003). The polymorphism in this population may be maintained by diversity already extant in the population. The lack of genetic differentiation between the Great Plains and Great Basin Swainson's hawk populations (Hull et al., 2008) helps support the idea that this polymorphism could be maintained through a large panmictic population. Despite the lack of genetic differentiation in this species, we observe an east-west cline in the proportion of dark and intermediate morphed individuals. This pattern is seen in several North American *Buteo* species, including Swainson's hawks, Red-tailed Hawks, and Broad-winged Hawks (*Buteo platypterus*, Wheeler, 2003). In fact, clines in

melanistic coloration are seen in numerous species, such as bannanaquits (*Coereba flaveola*, Wunderle Jr, 1981b, Wunderle Jr, 1981a, MacColl & Stevenson, 2003), barn owls (Roulin et al., 2009, Roulin, 2003), lesser snow geese (Cooch, 1961) and thinhorn sheep (*Orvis dalli* Nelson, Loehr et al., 2008)

While all of these species are widespread and have relatively large populations (Wheeler, 2003), the underlying pattern maintaining such clines is largely unknown. However, larger populations may occur in a greater number of habitats, producing GE interactions (Galeotti & Rubolini, 2004). In such cases, we would expect some morphs to have higher fitness in specific habitat types, but dispersal and subsequent genetic mixing may impede local adaption (e.g., Räsänen & Hendry, 2008). In fact, this mechanism has been implied for barn owls (Antoniazza et al., 2010), though there is not yet direct data on the specific fitness of morph types for a GE interaction. Whatever the mechanism, it seems likely that similar processes may have helped develop these polymorphisms across the genus *Buteo*. It is currently unclear what may have created the observed clines, and what mechanism, if any, is currently maintaining them. However, it seems that they are not maintained by differential fitness for this population.

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Literature Cited

- Akaike, H. (1973) Information Theory as an extension of the maximum likelihood principle. In: *Second international symposium on Information Theory*, (Petrov, B. N. & Csaki, F., eds.). pp. 267-281. Akademiai, Kaido.
- Allison, A. C. (1955) Aspects of polymorphism in man. Vol. 20. pp. 239. Cold Spring Harbor Laboratory Press.
- Antoniazza, S., Burri, R., Fumagalli, L., Goudet, J. & Roulin, A. 2010. Local adaptation maintains clinal variation in melanin-based coloration of European barn owls (*Tyto alba*). *Evolution* **9999**.
- Arcese, P. & Fitzner, R. E. (1982) Plumage polymorphism in Swainson's Hawk (*Buteo Swainsoni*): testing a hypothesis of apostatic selection of predators. pp. Pacific Northwest Labs., Richland, WA (USA).
- Arcos, J. M. 2007. Frequency-dependent morph differences in kleptoparasitic chase rate in the polymorphic arctic skua *Stercorarius parasiticus*. *Journal of Ornithology* **148**: 167-171.
- Baiao, P. C. & Parker, P. G. 2008. Maintenance of plumage polymorphism in Red-footed Boobies in the Galapagos Archipelago: Observations of mate choice and habitat association. *Condor* **110**: 544-548.
- Bates, D. & Maechler, M. 2009. lme4: Linear mixed-effects models using S4 classes. R package version 0.99375-32.

- Bloom, P. H., Henckel, J. L., Henckel, E. H., Schmutz, J. K., Woodbridge, B., Bryan, J. R., Anderson, R. L., Detrich, P. J. & Maechtle, T. L. 1992. The dho-gaza with great horned owl lure: An analysis of its effectiveness in capturing raptors. *Journal of Raptor Research* **26**: 167-178.
- Bond, A. B. & Kamil, A. C. 1998. Apostatic selection by blue jays produces balanced polymorphism in virtual prey. *Nature* **395**: 594-596.
- Briggs, C. W. (2007) Survival and nesting ecology of Swainson's hawks in Butte Valley, CA. In: *Natural Resources and Environmental Science*, Vol. M.Sc. pp. 99. University of Nevada, Reno, Reno.
- Briggs, C. W., Woodbridge, B. & Collopy, M. W. 2010a. Inheritance patterns of plumage morph in Swainson's Hawks. *Journal of Raptor Research* **44**: 232-235.
- Briggs, C. W., Woodbridge, B. & Collopy, M. W. 2010b. Temporal morph invariance of Swainson's Hawks. *Journal of Raptor Research* **44**: 70-73.
- Brommer, J. E., Ahola, K. & Karstinen, T. 2005. The colour of fitness: plumage coloration and lifetime reproductive success in the tawny owl. *Proceedings of the Royal Society B: Biological Sciences* **272**: 935.
- Burnham, K. P. & Anderson, D. R. 2002. *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York, New York.
- Caldow, R. W. G. & Furness, R. W. 1991. The relationship between kleptoparasitism and plumage polymorphism in the arctic skua *Stercorarius parasiticus* (L.). *Functional Ecology* **5**: 331-339.

- Chakarov, N., Boerner, M. & Kruger, O. 2008. Fitness in common buzzards at the cross-point of opposite melanin-parasite interactions. *Functional Ecology* **22**: 1062-1069.
- Choquet, R., Lebreton, J. D., Gimenez, O., Reboulet, A. M. & Pradel, R. 2009. U-CARE: Utilities for performing goodness of fit tests and manipulating Capture-REcapture data. *Ecography* **32**: 1071-1074.
- Choquet, R., Reboulet, A. M., Lebreton, J. D., Gimenez, O. & Pradel, R. (2005) U-CARE. 2.2 user's manual. CEFE, Montpellier, France. pp.
- Comendant, T., Sinervo, B., Svensson, E. I. & Wingfield, J. 2003. Social competition, corticosterone and survival in female lizard morphs. *Journal of Evolutionary Biology* **16**: 948-955.
- Cooch, G. 1961. Ecological aspects of the blue-snow goose complex. *The Auk* **78**: 72-89.
- England, A. S., Bechard, M. J. & Houston, C. S. (1997) Swainson's Hawk (*Buteo swainsoni*). In: *Birds of North America, No. 265*, (Poole, A. & Gill, F., eds.). pp. The American Ornithologists' Union, Washington, D.C.
- Fowlie, M. K. & Kruger, O. 2003. The evolution of plumage polymorphism in birds of prey and owls: The apostatic selection hypothesis revisited. *Journal of Evolutionary Biology* **16**: 577-583.
- Francis, C. M., Richards, M. H., Cooke, F. & Rockwell, R. F. 1992. Changes in survival rates of lesser snow geese with age and breeding status. *The Auk*: 731-747.
- Galeotti, P. & Rubolini, D. 2004. The niche variation hypothesis and the evolution of colour polymorphism in birds: a comparative study of owls, nightjars and raptors. *Biological Journal of the Linnean Society* **82**: 237-248.

- Galeotti, P., Rubolini, D., Dunn, P. O. & Fasola, M. 2003. Colour polymorphism in birds: Causes and functions. *Journal of Evolutionary Biology* **16**: 635-646.
- Gelman, A. & Rubin, D. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* **7**: 457-511.
- Gigord, L. D. B., Macnair, M. R. & Smithson, A. 2001. Negative frequency-dependent selection maintains a dramatic flower color polymorphism in the rewardless orchid *Dactylorhiza sambucina* (L.) Soo. *Proceedings of the National Academy of Sciences of the United States of America* **98**: 6253.
- Goldstein, G., Flory, K. R., Browne, B. A., Majid, S., Ichida, J. M., Burt Jr, E. H. & Grubb Jr, T. 2004. Bacterial degradation of black and white feathers. *The Auk* **121**: 656-659.
- Green, P. J. 1995. Reversible jump Markov chain Monte Carlo computation and Bayesian model determination. *Biometrika* **82**: 711-732.
- Gulland, F. M. D., Albon, S. D., Pemberton, J. M., Moorcroft, P. R. & Clutton-Brock, T. H. 1993. Parasite-associated polymorphism in a cyclic ungulate population. *Proceedings: Biological Sciences* **254**: 7-13.
- Hanson, M. T. & Coss, R. G. 1997. Age Differences in the Response of California Ground Squirrels (*Spermophilus beecheyi*) to Avian and Mammalian Predators*
1. *Journal of Comparative Psychology* **111**: 174-184.
- Hedrick, P. W., Ginevan, M. E. & Ewing, E. P. 1976. Genetic polymorphism in heterogeneous environments. *Annual Review of Ecology and Systematics* **7**: 1-32.
- Hori, M. 1993. Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. *Science* **260**: 216.

- Houston, C. S. 2005. Swainson's Hawk longevity, colour banding and natal dispersal. *Blue Jay* **63**: 31-39.
- Houtman, A. M. & Falls, J. B. 1994. Negative assortative mating in the white-throated sparrow, *Zonotrichia albicollis* - the tole of mate choice and intrasexual competition. *Animal Behaviour* **48**: 377-383.
- Hull, J. M., Anderson, R., Bradbury, M., Estep, J. A. & Ernest, H. B. 2008. Population structure and genetic diversity in Swainson's Hawks (*Buteo swainsoni*): implications for conservation. *Conservation Genetics* **9**: 305-316.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological monographs* **54**: 187-211.
- King, R. & Brooks, S. P. 2004. A classical study of catch-effort models for Hector's dolphins. *Journal of the American Statistical Association* **99**: 325-333.
- Krueger, O., Lindstrom, J. & Amos, W. 2001. Maladaptive mate choice maintained by heterozygote advantage. *Evolution* **55**: 1207-1214.
- Lank, D. B. 2002. Diverse processes maintain plumage polymorphisms in birds. *Journal of Avian Biology* **33**: 327-330.
- Levene, H. 1953. Genetic equilibrium when more than one ecological niche is available. *American Naturalist* **87**: 331-333.
- Levins, R. & MacArthur, R. 1966. The maintenance of genetic polymorphism in a spatially heterogeneous environment: variations on a theme by Howard Levene. *American Naturalist* **100**: 585-589.

- Loehr, J., Worley, K., Moe, J., Carey, J. & Coltman, D. 2008. MC1R variants correlate with thinhorn sheep colour cline but not individual colour. *Canadian Journal of Zoology* **86**: 147-150.
- Lunn, D. J., Best, N. & Whittaker, J. 2009. Generic reversible jump MCMC using graphical models. *Statistics and Computing* **19**: 395-408.
- Lunn, D. J., Thomas, A., Best, N. & Spiegelhalter, D. 2000. WinBUGS - a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and Computing* **10**: 325-337.
- MacColl, A. & Stevenson, I. 2003. Stasis in the morph ratio cline in the bananaquit on Grenada, West Indies. *Condor* **105**: 821-825.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* **73**: 255-261.
- Mayfield, H. 1975. Suggestions for calculating nest success. *Wilson Bulletin* **87**: 456-466.
- Meunier, J., Figueiredo Pinto, S., Burri, R. & Roulin, A. 2011. Eumelanin-based coloration and fitness parameters in birds: a meta-analysis. *Behavioral Ecology and Sociobiology*: 1-9.
- Mosher, J. A. & Henny, C. J. 1976. Thermal adaptiveness of plumage color in screech owls. *The Auk*: 614-619.
- Mundy, N. I. 2005. A window on the genetics of evolution: MC1R and plumage colouration in birds. *Proceedings of the Royal Society Biological Sciences Series B* **272**: 1633-1640.
- Newton, I. 1989. *Lifetime reproduction in birds*. Academic Press, New York.

- Nosil, P. 2008. Ernst Mayr and the integration of geographic and ecological factors in speciation. *Biological Journal of the Linnean Society* **95**: 26-46.
- O'Donald, P. 1983. The Arctic skua: A study of the ecology and evolution of a seabird. *Cambridge University Press, Cambridge (UK)*.
- Palmer, R. S. 1988. In: Handbook of North American Birds, vols. 4 and 5. *Diurnal raptors (Parts 1 and 2)*. Yale University Press, New Haven, CT.
- Paulson, D. R. 1973. Predator polymorphism and apostatic selection. *Evolution*: 269-277.
- Pimentel, R. A. 1979. *Morphometrics: the multivariate analysis of biological data*. Kendall/Hunt Publishing, Dubuque, Iowa, USA.
- Plummer, M., Best, N., Cowles, K. & Vines, K. 2006. CODA: convergence diagnostics and output analysis for MCMC. *R News* **6**: 7-11.
- Postma, E. & van Noordwijk, A. J. 2005. Gene flow maintains a large genetic difference in clutch size at a small spatial scale. *Nature* **433**: 65-68.
- Preston, C. R. 1980. Differential perch site selection by color morphs of the Red-tailed Hawk (*Buteo jamaicensis*). *Auk* **97**: 782-789.
- Räsänen, K. & Hendry, A. 2008. Disentangling interactions between adaptive divergence and gene flow when ecology drives diversification. *Ecology Letters* **11**: 624-636.
- Robinson, S. R. 1980. Antipredator behaviour and predator recognition in Belding's ground squirrels. *Animal Behaviour* **28**: 840-852.
- Roulin, A. 2003. Geographic variation in sexual dimorphism in the barn owl *Tyto alba*: a role for direct selection or genetic correlation? *Journal of Avian Biology* **34**: 251-258.

- Roulin, A., Wink, M. & Salamin, N. 2009. Selection on a eumelanic ornament is stronger in the tropics than in temperate zones in the worldwide distributed barn owl. *Journal of Evolutionary Biology* **22**: 345-354.
- Schmidt, J. H., Walker, J. A., Lindberg, M. S., Johnson, D. S. & Stephens, S. E. 2010. A General Bayesian Hierarchical Model for Estimating Survival of Nests and Young. *The Auk* **127**: 379-386.
- Schmutz, S. M. & Schmutz, J. K. 1981. Inheritance of color phases of ferruginous hawks. *Condor* **83**: 187-189.
- Sharp, C. S. 1902. Nesting of Swainson Hawk. *Condor* **4**: 116-118.
- Spiegelhalter, D. J., Best, N. G., Carlin, B. P. & Linde, A. V. d. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society B* **64**: 583-639.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, England.
- Sturtz, S., Ligges, U. & Gelman, A. 2005. R2WinBUGS: a package for running WinBUGS from R. *Journal of Statistical Software* **12**: 1-16.
- Team, R. D. C. (2009) R: A language and environment for statistical computing. pp. R Foundation for statistical computing, Vienna, Austria.
- Ward, J. M., Ruxton, G. D., Houston, D. C. & McCafferty, D. J. 2007. Thermal consequences of turning white in winter: a comparative study of red grouse *Lagopus lagopus scoticus* and Scandinavian willow grouse *L. l. lagopus*. *Wildlife Biology* **13**: 120-129.

- Wheeler, B. K. 2003. *Raptors of Western North America: The Wheeler Guides*. Princeton University Press, Princeton, NJ.
- White, G. C. & Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**: 120-138.
- Woodbridge, B. (1991) Habitat selection by nesting Swainson's hawk: a hierarchical approach. Vol. M.Sc. Thesis. pp. 80. Oregon State University, Corvallis, OR.
- Wunderle Jr, J. 1981a. An analysis of a morph ratio cline in the bananaquit (*Coereba flaveola*) on Grenada, West Indies. *Evolution*: 333-344.
- Wunderle Jr, J. 1981b. Movements of adult and juvenile Bananaquits within a morph-ratio cline. *The Auk* **98**: 571-577.

Table 1. Multistate model results of adult apparent survival of Swainson's hawks in Butte Valley, CA. AIC_c value for the best ranked model was 3089.3.

| Model ¹ | AIC _c | | Num. | Deviance |
|--------------------------------|------------------|---------|------|----------|
| | ΔAIC_c | Weights | Par | |
| T+T ² *morph | 0 | 0.76 | 17 | 3054.8 |
| T+T ² +morph | 4.3 | 0.09 | 11 | 3071.3 |
| T+T ² +Intermediate | 4.3 | 0.09 | 9 | 3075.4 |
| T+T ² *Intermediate | 5.5 | 0.04 | 11 | 3072.6 |
| T+T ² | 10.6 | 0.00 | 8 | 3083.8 |
| T+T ² +Light | 12.0 | 0.00 | 9 | 3083.2 |
| T+T ² +Dark | 12.2 | 0.00 | 9 | 3083.3 |
| Null | 14.5 | 0.00 | 6 | 3091.8 |

¹T, a temporal trend through the course of the study; T², a quadratic temporal trend;

morph, the morph category of the individual; Light, Light morph adult;

Intermediate, intermediate/rufous morph adult; dark dark morph adult.

Table 2. Model-averaged adult apparent survival beta estimates from Program MARK from a multistate model examining different adult apparent survival rates for Swainson's hawks nesting in Butte Valley, CA. All models also include previously documented quadratic temporal trends. Betas are model-averaged intercept values from all models including the morph term listed (Table 1).

| Morph | Beta | SE |
|--------------|------|------|
| Light | 0.42 | 0.21 |
| Intermediate | 0.04 | 0.20 |
| Dark | 0.50 | 0.21 |

Table 3. Marginal posterior probabilities for variables used in reversible jmp variable selection analysis (RJCMC) of daily nest survival of different morph classes of Swainson's hawks nesting in Butte Valley, CA.

| Model ¹ | Male | Female |
|--------------------------|------|--------|
| Light | 0.55 | 0.13 |
| Intermediate | 0.22 | 0.10 |
| Dark | 0.15 | 0.12 |
| Proportion | 0.24 | .013 |
| % Light Offspring | | 0.50 |
| % Intermediate Offspring | | 0.32 |
| % Dark Offspring | | .036 |

¹Light, Light morph adult; Intermediate, intermediate/rufous morph adult; dark dark morph adult; proportion, the proportion of the population that has the same morph as the attendant adult; % Offspring, the expected proportion of offspring for that nesting attempt based on a one-locus, two-allele trait.

Table 4. Model selection for number of offspring produced per breeding attempt from a mixed model regression. Models within 4 AIC_c units of the best model are shown. AIC_c for the best ranked model was 46.0.

| Model ¹ | ΔAIC_c | Model Weight | Number of Parameters | Deviance |
|--------------------|----------------|--------------|----------------------|----------|
| Null | 0.0 | 0.24 | 1 | 40.0 |
| Year | 0.2 | 0.22 | 2 | 38.2 |
| %Light Offspring | 1.9 | 0.09 | 2 | 39.9 |
| % Intermediate | | | 2 | |
| Offspring | 1.9 | 0.09 | | 39.9 |
| Male proportion | 1.9 | 0.09 | 2 | 39.9 |
| Female proportion | 2.0 | 0.09 | 2 | 40.0 |
| % Dark offspring | 2.0 | 0.09 | 2 | 40.0 |
| Female morph | 3.8 | 0.04 | 3 | 39.8 |
| Male morph | 3.9 | 0.03 | 3 | 39.9 |

¹Light, Light morph adult; Intermediate, intermediate/rufous morph adult; Dark, dark morph adult; proportion, the proportion of the population that has the same morph as the attendant adult; % Offspring, the expected proportion of offspring for that nesting attempt based on a one-locus, two-allele trait; Male morph, morph of the attendant male; Female morph, morph of the attendant female; Year, a temporal trend through the course of the study.

Table 5. Model selection results for generalized linear models of lifetime reproductive success of Swainson's hawks in Butte Valley, CA. AIC_c for the best ranked model was 462.2.

| Model ¹ | ΔAIC_c | Weight | Number of Parameters | Deviance |
|--------------------|----------------|--------|----------------------|----------|
| Year | 0 | 0.99 | 2 | 456.2 |
| Year*Morph | 4.8 | 0.00 | 6 | 453.0 |
| Null | 23.8 | 0.00 | 1 | 482.0 |
| Morph | 26.8 | 0.00 | 3 | 481.0 |

¹Year, temporal trend through the course of the study; Morph, morph category of the individual; Null, a null model.

Table 6. Model selection results for probability of recruitment of nestling Swainson's hawks into the breeding population. Models within 4 AIC_c units are shown. Results are from a mixed-model logistic regression. AIC_c for the best ranked model was 213.8.

| Model ¹ | ΔAIC_c | Model Weight |
|--------------------------|----------------|--------------|
| Year | 0.0 | 0.20 |
| Null | 0.4 | 0.16 |
| Year+Male Proportion | 1.1 | 0.12 |
| Male Proportion | 1.5 | 0.10 |
| Year+Female Proportion | 2.0 | 0.07 |
| % Dark Offspring | 2.2 | 0.07 |
| % Light Offspring | 2.3 | 0.06 |
| % Intermediate Offspring | 2.4 | 0.06 |
| Female Proportion | 2.4 | 0.06 |
| Male Morph | 3.4 | 0.04 |
| Female Morph | 3.8 | 0.03 |

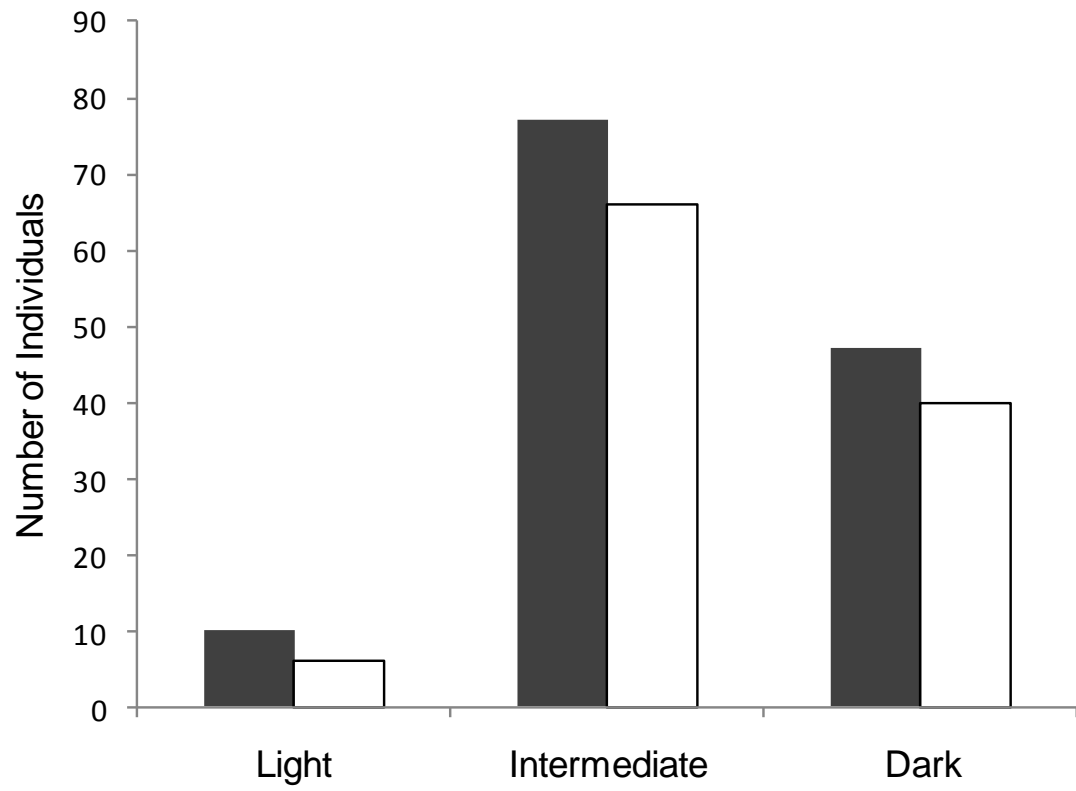
¹Morph, the category of the attendant breeder; proportion, the proportion of the population that has the same morph as the attendant adult; % Offspring, the expected proportion of offspring for that nesting attempt based on a one-locus, two-allele trait; Year, a temporal trend over the course of the study.

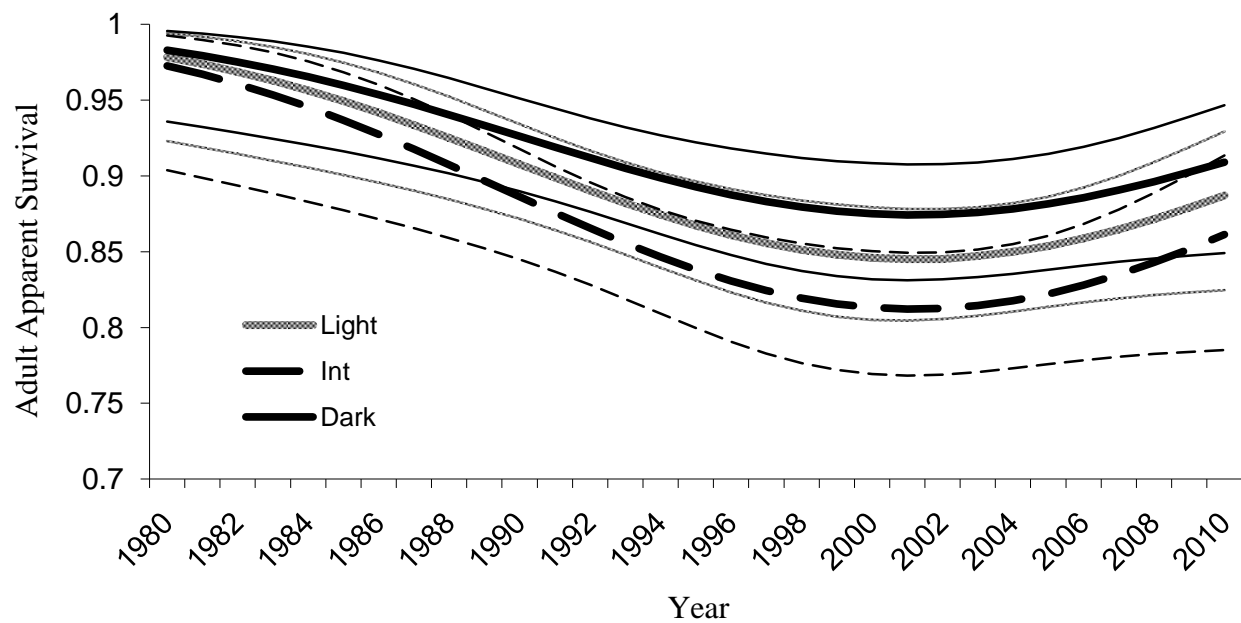
Figure 1. Morph distribution of all breeding and marked and photographed male (grey) and female (white) Swainson's hawks trapped in Butte Valley, California from 1979-2010.

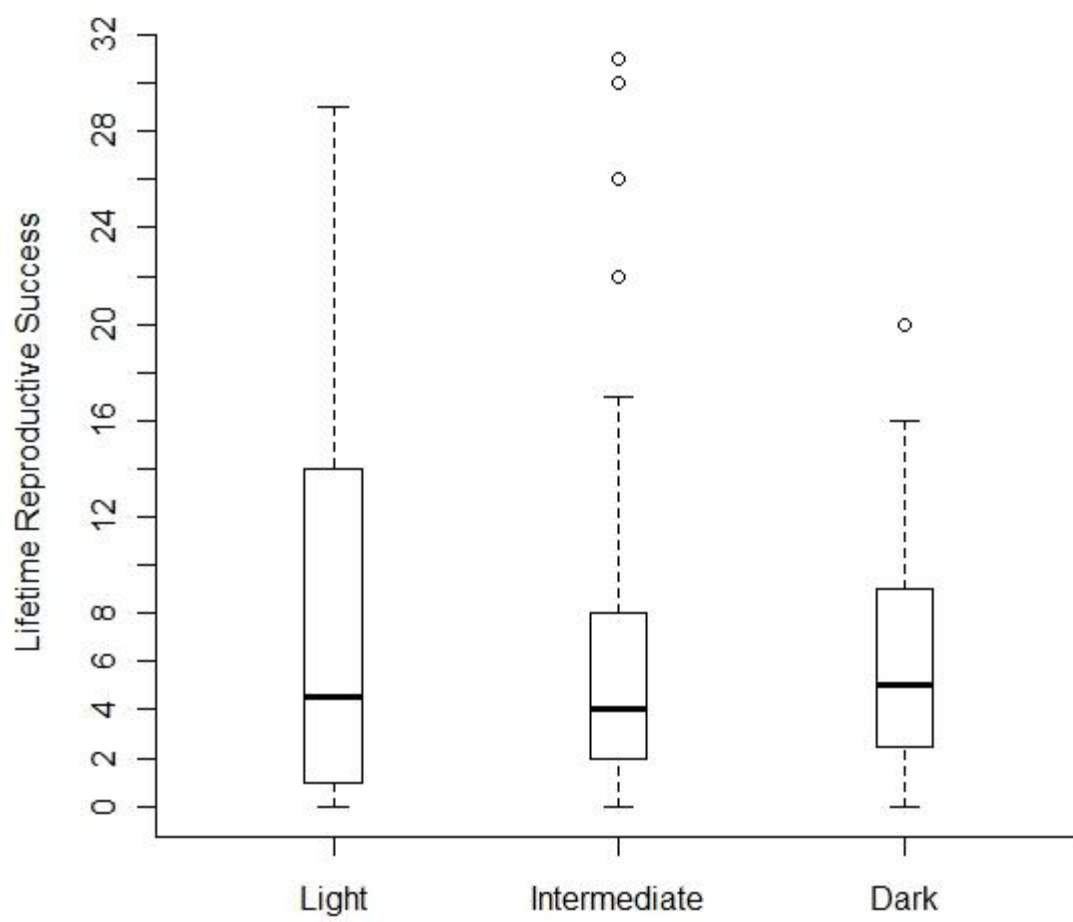
Figure 2. Model-averaged estimates of adult apparent survival of different plumage morphs from multistate modeling of Swainson's hawks marked in Butte Valley, California from 1979-2010.

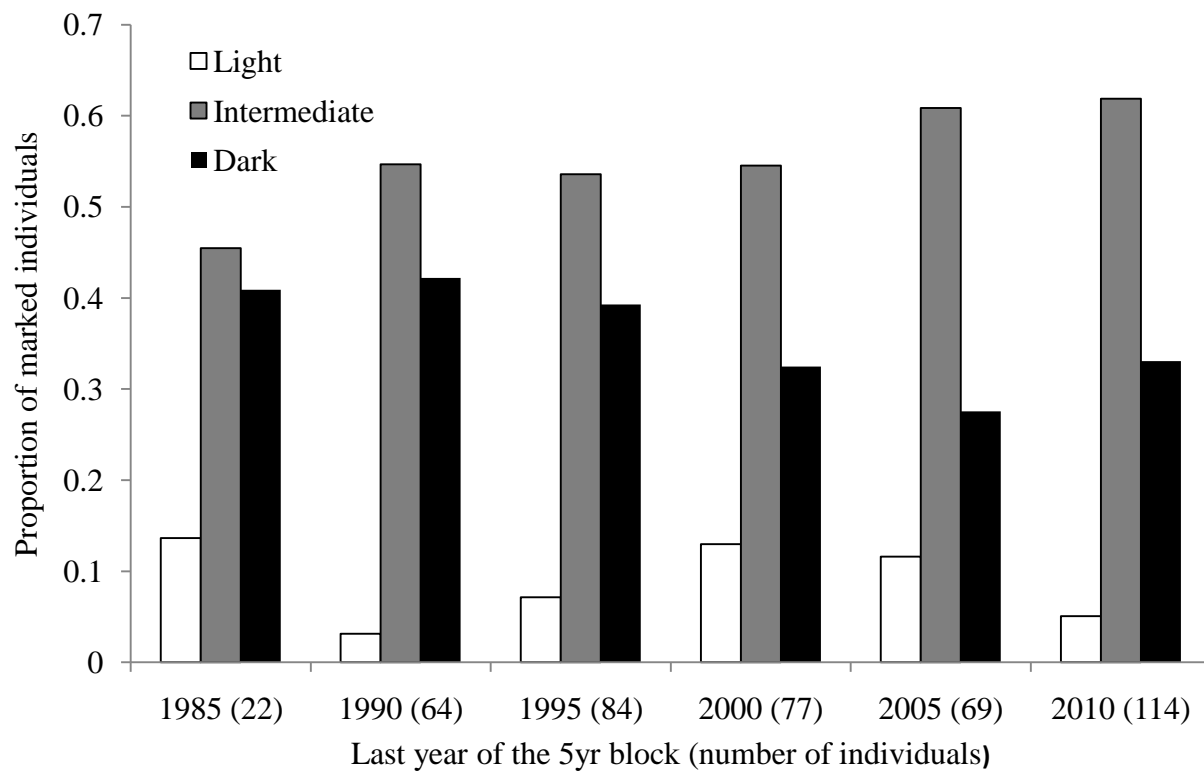
Figure 3. Boxplot of lifetime reproductive success for female light (n=6), intermediate (n=33), and dark (n=25) morph Swainson's hawks banded in Butte Valley, Ca from 1979-2010. Individuals that were not observed for >2 years of the study were excluded to ensure individuals that were still breeding were not included. Circles indicate statistical outliers.

Figure 4. Proportion of adult individuals of light (white), intermediate (grey), and dark (black) morph Swainson's hawks observed nesting in/around Butte Valley, CA. Unique Individual observations were grouped into 5yr blocks.









Chapter 3 - Oedipal Complexes and Sexual Selection Maintain a Polymorphism

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Abstract

Persistent plumage polymorphisms are differences in plumage within the same age and sex class in a population. Many mechanisms maintaining polymorphisms have been proposed. We investigated sexual selection in a population of Swainson's Hawks in Butte Valley, California, USA. Specifically, we determined if individuals selected mates based on their own phenotype or imprinting of parental phenotypes. We found that Swainson's hawks do not select mates based on their own phenotype. Females do not select mates based on a parental phenotype; however, males do select mates based on their maternal phenotype. Males selected females based on morph more consistently than we would expect by chance, demonstrating males are selecting for the maternal phenotype. Males that mated with females different than the maternal phenotype had significantly lower lifetime reproductive success (9.2 ± 1.9 , versus 3.7 ± 1.0 fledglings). These individuals may have been poorer quality individuals, as evidenced by their lower number of breeding attempts. Thus, this polymorphism may be maintained via sexual selection of males selecting for females that are similar to the maternal phenotype.

Key words – assortative mating, color polymorphism, imprinting, mate choice, Swainson's Hawk

Introduction

Persistent plumage polymorphisms, or morphs, are variations in plumage found within the same and age class within the same population, and are thought to be stable over time. Explanations of how morphs, and polymorphisms in general, persist over time have propagated a number of hypotheses to explain their existence in the face of genetic drift or natural selection (e.g., Fowlie and Kruger 2003, Galeotti et al. 2003, Galeotti and Rubolini 2004, Roulin and Wink 2004). Hypotheses often involve explanations of differences in fitness or life-history strategies, such as heterozygote advantage (Krüger et al. 2001) or negative frequency dependant selection (Arcos 2007).

Alternatively, sexual selection may maintain polymorphisms, with hypotheses often centered around assortative mating and imprinting. Assortative mating occurs when individuals select mates of the same or similar phenotypes to themselves (i.e. positive) or of dissimilar phenotypes (i.e. negative). Positive assortative mating based on coloration has been observed in a number of species (Cooke et al. 1976, Abraham et al. 1983, Andersson 1998, Salzburger et al. 2006), and may lead to subsequent genetic divergence between groups (Kirkpatrick 2000). Disassortive mating has similarly been described in a number of species (Throneycroft 1975) and can lead to the maintenance of polymorphisms (Knapton and Falls 1983).

Imprinting on parental phenotypes may also aid the maintenance of polymorphisms. Imprinting on parental phenotypes has been observed in lesser Snow Geese (*Anser c. caenescenens*), with individuals having strong preference for parental phenotypes (Cooke et al. 1972, Cooke and McNally 1975). Imprinting has also been

cited as a potential mechanism for maintaining polymorphisms when other selective forces are not sufficient to maintain the persistent polymorphism (Krüger et al. 2001).

Studies have examined both fitness (Roulin et al. 2003) differences between morph types (Meunier et al. 2011) and sexual selection (Cooke and McNally 1975, Hugie and Lank 1997, Tuttle 2003). Other research has also examined correlates of polymorphisms across species, concluding that polymorphisms may be aided by large populations (Frankham 1996, Fowlie and Kruger 2003), range size (Fowlie and Kruger 2003), and prey base (Roulin and Wink 2004). However, few studies have tried to examine the maintenance of morphs within a species (Krüger et al. 2001, Brommer et al. 2005, Antoniazza et al. 2010). Polymorphisms are particularly common among raptors, occurring in approximately 38.5% of species in *Strigidae* and 22.1% of species in *Accipitridae* (Galeotti et al. 2003), and therefore have been the subject of a number of investigations on morphs (Fowlie and Kruger 2003, Galeotti and Rubolini 2004, Brommer et al. 2005). Relatively few studies, however, have tried to determine if mating patterns were nonrandom in raptors (Dunkle 1977, Roulin et al. 2003).

We take advantage of a 32-year dataset of Swainson's Hawks (*Buteo swainsoni*) to examine the hypothesis of non-random mating, its fitness consequences, and the ability of our patterns to maintain a plumage polymorphism in a population of Swainson's Hawks. Swainson's Hawks, in particular are well known for plumage polymorphisms (Wheeler 2003). There appears to be a continuous gradation in melanization in plumage of the belly, flanks and underwing coverts from individuals that are completely light to completely dark (Wheeler 2003); however, individuals are generally grouped into 3 categories; light, intermediate and dark. These categories follow a one-locus, two-allele

inheritance pattern (Briggs et al. 2010a) that has been found in other buteo species, including Ferruginous Hawks (*Buteo regalis*, Schmutz and Schmutz 1981) and Common Buzzards (*Buteo buteo*, Krüger et al. 2001). Further, morph does not change over the course of an adult individual's life (Briggs et al. 2010b), indicating morph is genetically determined, or determined early in life. There are no significant differences in proportions of morph types between the sexes (Briggs et al., in review). Previous analyses have also demonstrated that there are no differences between components of fitness between morph classes, with individuals of each morph class having the same adult apparent survival, reproduction, lifetime reproductive success, and rates of offspring recruitment (Briggs et al., in review). Therefore, in this paper we specifically examine assortative mating and imprinting in this population to explain the maintenance of morphs. We expect sexual selection to provide the mechanism for maintaining morphs, as Dunkle (1977) found positive assortative mating in a population of Swainson's Hawks in Wyoming.

Methods

Field Methods

We monitored a population of Swainson's Hawks in Butte Valley, California from 1979-2010. Adults were individually color marked using unique 2-digit color bands and a US Geological Survey (USGS) aluminum band. Adults were trapped using dho-gaza style net with a great-horned owl lure (*Bubo virginianus*, Bloom et al. 1992) or a bal-charti baited with mice. Trapped adults were photographed opportunistically with

one wing open to document plumage. Sex was determined by examining individuals for a brood patch, by size measurements, and through observation of copulatory behavior.

Territories were monitored annually, and nest sites were located by watching for nest building, mating behavior and territoriality (April – May); in the summer months, nests were found by watching for prey deliveries to the nest site. The nest tree was climbed approximately two weeks after the mean hatch date to determine nesting status and determine chick age. Nestlings were banded with standard USGS aluminum bands approximately 1-2 weeks before fledging. Chicks typically do not return to the study area for a minimum of 2-3 years, when they begin breeding. At that time, we attempt to trap all individuals with USGS aluminum bands for confirmation of identification.

We used photographs of adult birds to place them into one of three categories; light, intermediate/rufous, and dark (Wheeler 2003, Briggs et al. 2010b). Briefly, light individuals had little or no melanization in the belly, flanks or underwing coverts; intermediate individuals had considerable melanization in the belly, flanks and underwing coverts, but it was still possible to differentiate the bib from the belly and white patches were still visible in all areas; dark individuals had completely melanized belly and flanks, such that the belly and flanks were not distinguishable from the dark bib.

Assortative Mating

We first examined assortative mating by examining mate choice patterns in the population during the course of the study. Specifically, we used a G-test to compare the observed pairings of light, intermediate and dark individuals with an expected frequency

of random pairings. We used a G-test to account for low expected values (i.e. <5) for certain pairings (Sokal and Rohlf 1995). To obtain random pairings we used the male and female morph frequencies and randomized pairings 10,000 times, and calculated the average number of pairings in each of the pair combinations (e.g., light x light, light x intermediate, etc.). In cases where individuals had more than one mate over the course of the study (e.g., due to death of a mate or divorce), we used only the first mate in the analysis to avoid pseudo-replicating individuals.

Imprinting

We examined imprinting in Swainson's Hawks using individuals with at least one known parental morph and known mates. Therefore, the analysis was restricted to breeding individuals for which we knew the maternal and/or paternal phenotype(s), as well as the morph of the individuals mate(s). First, we examined the correlation between an individual's mate phenotype and their parental phenotype, using an ordinal regression from the `gnlm` library in R 2.10.1 (R Development Core Team 2009).

We used the kappa statistic (κ , Cohen 1960) to determine how well mate choice matched parental morph by taking into account the agreement we would observe by chance. κ examines the diagonal of a confusion matrix, taking chance agreement into account and producing a value ranging from 0-1, where 1 would indicate perfect agreement (i.e. all elements of the matrix were on the diagonal). The expected mate choice could be skewed because of small sample sizes. Therefore we used the proportions of morphs from the entire population to adjust our expected values of possible mates ($\kappa(\omega)$) by adjusting expected proportion based on the population

proportions of each morph. A $\kappa(\omega)$ value of greater than 0.80 reflected nearly perfect agreement between parental morph and mate morph, where 1.0 reflects a perfect correlation (Landis and Koch 1977).

Mate Choice Consistency

If individuals have a preference for a specific phenotype (e.g., based on either their own phenotype or parental phenotype) we expect that individuals should select mates of a given phenotype more consistently than we would expect by chance. Therefore we also examined the history of mate choice of all individuals regardless of whether we knew a parental phenotype. We compared the consistency of mate's morph in both males and females utilizing individuals that chose more than one mate over the course of the study. While Swainson's Hawks generally pair with the same mate every year (B. Woodbridge unpub. data), occasionally a pair will divorce or one member of a pair will die, allowing us to assess mate choice consistency when individuals choose new mates. If an individual chose a mate of different morph types we assigned a 1, and choosing a mate of the same morph type we assigned a 0. We averaged mate choices across individuals. We then compared observed matings with what we would expect based on random choice given the proportions of each morph in the population. If an individual had more than two mates of known morph over the course of its lifetime, we randomly choose two mates. Random matings were determined by randomly choosing pairs of two males (i.e. female random mate choice) or two females (i.e. male random mate choice), and again determining if there was a difference in the morphs. The number of pairs selected was the same as the number of data points observed for males and

females, respectively. This process was repeated 10,000 times to obtain average and SE of random mate choices for both males and females. We then compared mate consistency with our expectation of mate consistency if individuals chose mates at random using a t-test separately for males and females.

Lifetime Reproductive Success

We used lifetime reproductive success (LRS) to examine the relationship between fitness and mate choice. We only included individuals that were likely dead (i.e. had not been observed for ≥ 3 yrs to avoid inclusion of individuals whose LRS measurement was incomplete. Specifically, we tested if LRS was related to choosing a mate of similar morph category as the individual or as either maternal or paternal phenotypes. We determined if an individual mated with the same (1) or different (0) morph as its mother and father, and regressed each of those against LRS separately for males and females. We used a quasipoisson link to account for overdispersion of the data (i.e. a variance greater than the mean) in R 2.10.1.

Results

From 1979-2010, we were able to trap and photograph 337 (182 male and 155 female) adult Swainson's Hawks, and 117 of these were recruited from within the population, and 65 had at least one marked parent. There were 109 pairings between individuals where the morph of both members of the pair was documented photographically. There was no significant selection for a mate based on an individual's morph class ($G=9.3$, $df=5$, $P=0.10$; Table 1).

We found that males generally selected mates with a maternal morph phenotype (Table 2, $n = 26$, $\kappa(\omega) = 0.88$); however, females did not select for either maternal ($n = 19$, $\kappa(\omega) = 0.13$) or paternal ($n = 24$, $\kappa(\omega) = 0.38$) phenotypes. Likewise, males did not select for paternal phenotypes (Table 2, $n = 29$, $\kappa(\omega) = 0.37$).

In cases where individuals were observed and recorded with more than one mate, males also selected for female morph more consistently than would be expected by chance ($n=24$, $t=3.62$, $P<0.001$). Males chose mates of a different morph less frequently than females (0.21 ± 0.08 , 0.73 ± 0.08). In contrast, females selected mates at random with respect to morph ($n=27$, $t=1.00$, $P=0.20$).

Differences between mates and parental morphs was not a significant predictor of LRS for females. In contrast, males that mated with females different than their maternal morph type (LRS = 3.7 ± 1.0 fledglings, $n=9$) had a significantly lower LRS than those that mated with females the same as their maternal morph (9.2 ± 1.9 fledglings, $n=10$; Table 3).

Discussion

We found that male Swainson's Hawks breeding in our population preferred females with a maternal phenotype, suggesting an Oedipal complex wherein males are attracted to their mother and this can lead to choosing mates based on that fixation (Freud 1924). In contrast, females do not select males based on either maternal or paternal phenotype. This result suggests that male offspring imprint on their maternal phenotype and have a strong preference for that phenotype. While our sample sizes where individuals have known parents and a known mate are small, we were also able to

demonstrate that male individual mate choice is more consistent than we would expect by chance. If males do imprint on a maternal phenotype, it is reasonable to expect that individual mate choice should be consistent over time as males select for their preferred phenotype. Again, sample sizes were low due to the relatively high mate fidelity and high individual apparent survival, but this line of evidence provides clear support for our hypothesis that males are imprinting on the maternal phenotype.

Males did not universally select female mates based on maternal phenotype; however, those that chose a mate with a different phenotype had a lower LRS. This lower LRS was primarily the result of lower apparent survival rather than lower reproduction, suggesting that these individuals had lower individual quality. If they had lower individual quality, they may not be able to be as choosy in mate selection, and have to settle for a less desirable mate. Alternatively, apparent survival may be lower because males that could not obtain a mate of the preferred morph were more likely to move out of the study area, biasing their LRS low. Either way, an inability to obtain a mate with the maternal phenotype resulted in males with decreased LRS.

Increasing parental investment in offspring should lead to increases in choosiness in mates (Trivers 1972) to maximize reproductive returns (Gwynne 1993, Reinhold et al. 2002). As male Swainson's Hawks are the primary food provider during the incubation and early brood-rearing periods (Fitzner 1980), it is reasonable to suspect that males should invest a similar amount to females (Breitwisch 1989), and should therefore have criteria for selecting a mate. In contrast, females may be choosy, but have other criterion for mate choice such as territory productivity, competitor abundance or mate experience.

The driver to develop an imprinting mechanism and why only males appear to actually imprint is unclear. We have found no evidence for differences in nest survival, number of offspring fledged, number of offspring recruited or LRS between the morph classes (Briggs et al, in review), and conclude there are no fitness differences between the morphs. However, there was some evidence that adult dark morph apparent survival was slightly higher in our study population, although confidence intervals were overlapping for the model-averaged results. Without a demonstrable fitness difference across morph types, selecting a mate based on a phenotype seems arbitrary and could be the result of prior selective pressures no longer extant in the population. Alternatively, there may be benefits for different morphs in different areas and, on average, the fitness does not differ between classes. While we could not find such interactions in our fitness modeling, even subtle results could have large implications during the course of a species' development.

The increased frequency of intermediate and dark Swainson's Hawks from east to west across the range suggests there is a mechanism (e.g., thermal ecology) maintaining the morphs. Additionally, a slight survival advantage for dark individuals in the western edge of the range may indicate a phenotype-environment interaction (Briggs et al., in review). Therefore, as documented natal dispersal distances appear to be small relative to the range of the species (Briggs et al., in review, England et al. 1997), male preference may aid offspring fitness by trying to match offspring with the most appropriate environment. On the east coast, if light morph individuals also have a slight adult survival advantage then this male preference may help increase an individual's fitness by increasing the likelihood that its offspring are well suited for the environment in which they are likely going to breed. A similar light-to-dark cline is observed in other species

of buteos in North America (Wheeler 2003), suggesting there is a common mechanism found among these species that could be the ultimate cause of this gradation of morphs across the continent, and sexual selection may just be the proximate mechanism.

Alternatively, a mechanism that has been suggested for imprinting on a parental phenotype is the prevention of interspecific matings (i.e. hybridization avoidance, Pryke and Griffith 2007). In fact, Swainson's Hawks do hybridize with Red-tailed Hawks (*Buteo jamaciensis*), and both sexes appear to hybridize in the wild (Hull et al. 2008). However, neither mechanism explains why only males imprint on a parental phenotype.

In contrast to the imprinting results, we did not find any evidence for either positive or negative assortative mating, unlike in a previous study (Dunkle 1977); however, our results corroborate at least one other study of assortative mating in Swainson's Hawks (Arcese and Fitzner 1982). While imprinting may lead to assortative mating (Cooke and McNally 1975), it did not in this population.

These results provide unique insight into a long-lived vertebrate with delayed breeding, and help explain what is maintaining a polymorphism in this population. Few studies are able to detect significant numbers of recruits and the relatively high recruitment rates in this population and long-term nature of this study allow us to test beyond just assortative mating to further our understanding of sexual selection. These results also suggest caution for studies that cannot assess effects, such as imprinting, on mate selection. For example, Baião and Parker (2008) found no evidence of assortative mating in pairs of Red-footed Boobies (*Sula sula*). However, imprinting may not result in apparent assortative mating and the authors should not have ruled out nonrandom mating as a potential mechanism to maintain morphs in their study. While we also did

not observe assortative mating, nonrandom mating does seem to play a significant role in maintaining multiple morphs in our population. We provide several lines of evidence indicating that there is sexual selection in this population, and that selection pressure helps maintain a polymorphism in this population.

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Literature Cited

- Abraham, K. F., C. D. Ankney, and H. Boyd. 1983. Assortative mating by brant. *The Auk* **100**:201-203.
- Andersson, S. 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proceedings of the Royal Society B: Biological Sciences* **265**:445.
- Antoniazza, S., R. Burri, L. Fumagalli, J. Goudet, and A. Roulin. 2010. Local adaptation maintains clinal variation in melanin-based coloration of European barn owls (*Tyto alba*). *Evolution* **64**:1944-1954.
- Arcese, P. and R. E. Fitzner. 1982. Plumage polymorphism in Swainson's Hawk (*Buteo swainsoni*): testing a hypothesis of apostatic selection of predators. Pacific Northwest Labs., Richland, WA (USA).

- Arcos, J. M. 2007. Frequency-dependent morph differences in kleptoparasitic chase rate in the polymorphic arctic skua *Stercorarius parasiticus*. *Journal of Ornithology* **148**:167-171.
- Baião, P. C. and P. G. Parker. 2008. Maintenance of plumage polymorphism in red-footed Boobies in the Galápagos Archipelago: observations of mate choice and habitat association. *The Condor* **110**:544-548.
- Bloom, P. H., J. L. Henckel, E. H. Henckel, J. K. Schmutz, B. Woodbridge, J. R. Bryan, R. L. Anderson, P. J. Detrich, and T. L. Maechtle. 1992. The dho-gaza with great horned owl lure: An analysis of its effectiveness in capturing raptors. *Journal of Raptor Research* **26**:167-178.
- Breitwisch, R. 1989. Mortality patterns, sex ratios, and parental investment in monogamous birds. *Current ornithology* **6**:1-50.
- Briggs, C. W., B. Woodbridge, and M. W. Collopy. 2010a. Inheritance patterns of plumage morph in Swainson's Hawks. *Journal of Raptor Research* **44**:232-235.
- Briggs, C. W., B. Woodbridge, and M. W. Collopy. 2010b. Temporal morph invariance of Swainson's Hawks. *Journal of Raptor Research* **44**:70-73.
- Brommer, J. E., K. Ahola, and T. Karstinen. 2005. The colour of fitness: plumage coloration and lifetime reproductive success in the tawny owl. *Proceedings of the Royal Society B: Biological Sciences* **272**:935-940.
- Cohen, J. 1960. A coefficient of agreement for nominal scales. *Educational and psychological measurement* **20**:37-46.
- Cooke, F., G. H. Finney, and R. F. Rockwell. 1976. Assortative mating in lesser snow geese (*Anser caerulescens*). *Behavior Genetics* **6**:127-140.

- Cooke, F. and C. M. McNally. 1975. Mate selection and colour preferences in lesser snow geese. *Behaviour* **53**:151-170.
- Cooke, F., P. J. Mirsky, and M. B. Seiger. 1972. Color preferences in the lesser snow goose and their possible role in mate selection. *Canadian Journal of Zoology* **50**:529-536.
- Dunkle, S. W. 1977. Swainson's hawks on the Laramie Plains, Wyoming. *The Auk* **94**:65-71.
- England, A. S., M. J. Bechard, and C. S. Houston. 1997. Swainson's Hawk (*Buteo swainsoni*).in A. Poole and F. Gill, editors. *Birds of North America*, No. 265. The American Ornithologists' Union, Washington, D.C.
- Fitzner, R. E. 1980. Behavioral ecology of the Swainson's Hawk (*Buteo swainsoni*) in Washington. Pac. NW Lab.
- Fowlie, M. K. and O. Kruger. 2003. The evolution of plumage polymorphism in birds of prey and owls: The apostatic selection hypothesis revisited. *Journal of Evolutionary Biology* **16**:577-583.
- Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. *Conservation Biology* **10**:1500-1508.
- Freud, S. 1924. The dissolution of the Oedipus complex. *Standard Edition* **19**:243-258.
- Galeotti, P. and D. Rubolini. 2004. The niche variation hypothesis and the evolution of colour polymorphism in birds: a comparative study of owls, nightjars and raptors. *Biological Journal of the Linnean Society* **82**:237-248.
- Galeotti, P., D. Rubolini, P. O. Dunn, and M. Fasola. 2003. Colour polymorphism in birds: Causes and functions. *Journal of Evolutionary Biology* **16**:635-646.

- Gwynne, D. T. 1993. Food quality controls sexual selection in Mormon crickets by altering male mating investment. *Ecology* **74**:1406-1413.
- Hugie, D. and D. Lank. 1997. The resident's dilemma: a female choice model for the evolution of alternative mating strategies in lekking male ruffs (*Philomachus pugnax*). *Behavioral Ecology* **8**:218-225.
- Hull, J. M., R. Anderson, M. Bradbury, J. A. Estep, and H. B. Ernest. 2008. Population structure and genetic diversity in Swainson's Hawks (*Buteo swainsoni*): implications for conservation. *Conservation Genetics* **9**:305-316.
- Kirkpatrick, M. 2000. Reinforcement and divergence under assortative mating. *Proceedings of the Royal Society B: Biological Sciences* **267**:1649-1655.
- Knapton, R. W. and J. B. Falls. 1983. Differences in parental contribution among pair types in the polymorphic white-throated sparrow. *Canadian Journal of Zoology* **61**:1288-1292.
- Krüger, O., J. Lindstrom, and W. Amos. 2001. Maladaptive mate choice maintained by heterozygote advantage. *Evolution* **55**:1207-1214.
- Landis, J. R. and G. G. Koch. 1977. The measurement of observer agreement for categorical data. *Biometrics* **33**:159 - 174.
- Meunier, J., S. Figueiredo Pinto, R. Burri, and A. Roulin. 2011. Eumelanin-based coloration and fitness parameters in birds: a meta-analysis. *Behavioral Ecology and Sociobiology*:1-9.
- Pryke, S. R. and S. C. Griffith. 2007. The relative role of male vs. female mate choice in maintaining assortative pairing among discrete colour morphs. *Journal of Evolutionary Biology* **20**:1512-1521.

- Reinhold, K., J. Kurtz, and L. Engqvist. 2002. Cryptic male choice: sperm allocation strategies when female quality varies. *Journal of Evolutionary Biology* **15**:201-209.
- Roulin, A., B. Ducret, P.-A. Ravussin, and R. Altwegg. 2003. Female colour polymorphism covaries with reproductive strategies in the tawny owl *Strix aluco*. *Journal of Avian Biology* **34**:393-401.
- Roulin, A. and M. Wink. 2004. Predator-prey relationships and the evolution of colour polymorphism: a comparative analysis in diurnal raptors. *Biological Journal of the Linnean Society* **81**:565-578.
- Salzburger, W., H. Niederstätter, A. Brandstätter, B. Berger, W. Parson, J. Snoeks, and C. Sturmbauer. 2006. Colour-assortative mating among populations of *Tropheus moorii*, a cichlid fish from Lake Tanganyika, East Africa. *Proceedings of the Royal Society B: Biological Sciences* **273**:257-266.
- Schmutz, S. M. and J. K. Schmutz. 1981. Inheritance of color phases of ferruginous hawks. *Condor* **83**:187-189.
- Sokal, R. R. and F. J. Rohlf. 1995. *Biometry*. WH Freeman and Company, New York.
- Team, R. D. C. 2009. *R: A language and environment for statistical computing*. R Foundation for statistical computing, Vienna, Austria.
- Throneycroft, H. B. 1975. A cytogenetic study of the white-throated sparrow, *Zonotrichia albicollis* (Gmelin). *Evolution* **29**:611-621.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136-179 in B. Campbell, editor. *Sexual Selection and the Descent of Man, 1871-1971*. Aldine, Chicago.

Tuttle, E. 2003. Alternative reproductive strategies in the white-throated sparrow: behavioral and genetic evidence. *Behavioral Ecology* **14**:425-432.

Wheeler, B. K. 2003. *Raptors of Western North America: The Wheeler Guides*. Princeton University Press, Princeton, NJ.

Table 1. Observed and expected pairings of light (L), intermediate (I) and dark (D)

Swainson's Hawks in Butte Valley, California, USA from 1979-2010. Expected pairings were calculated by randomly assigning mates to individuals over 1000 iterations.

| | L * L | L * I | L * D | I * I | I * D | D * D |
|----------|-------|-------|-------|-------|-------|-------|
| Observed | 2 | 18 | 2 | 38 | 32 | 17 |
| Expected | 1 | 11 | 4 | 38 | 42 | 13 |

Table 2. Observed relationship between an individual's parental plumage morph and their mates plumage morph for both male and female Swainson's Hawks breeding in Butte Valley, California, USA from 1979-2010.

| | | Maternal Morph | | | Paternal Morph | | |
|-------------------------|--------------|----------------|--------------|------|----------------|--------------|------|
| | | Light | Intermediate | Dark | Light | Intermediate | Dark |
| Male Mate Morph | Light | 1 | 0 | 0 | 0 | 1 | 0 |
| | Intermediate | 1 | 13 | 1 | 2 | 12 | 7 |
| | Dark | 0 | 0 | 9 | 0 | 3 | 4 |
| Female Mate Morph | Light | 0 | 0 | 1 | 0 | 1 | 0 |
| | Intermediate | 3 | 6 | 5 | 0 | 11 | 7 |
| | Dark | 0 | 2 | 2 | 2 | 3 | 0 |

Table 3. Average lifetime reproductive success (LRS) of individuals that selected mates with the same (S) or different (D) phenotypes as the maternal (M) and paternal (P) phenotypes of Swainson's Hawks breeding in Butte Valley, California, USA from 1979-2010.

| | Female | | | Male | | |
|----|--------|-----|----|------|-----|----|
| | mean | SE | n | mean | SE | n |
| SP | 16 | NA | 1 | 7.7 | 3.3 | 3 |
| DP | 5.8 | 1.6 | 14 | 6.8 | 1.7 | 13 |
| SM | 8.5 | 2.3 | 4 | 9.2 | 1.9 | 10 |
| DM | 7 | 2 | 12 | 3.7 | 1 | 9 |

Chapter 4 – Extra-pair Paternity in Swainson’s Hawks

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Abstract

Molecular techniques have demonstrated that social monogamy is not a good predictor of rates of extra-pair paternity for many bird species. While Passeriformes has been relatively well studied and generally demonstrated high extra-pair paternity rates, less is known about extra-pair paternity rates in other groups. We examined extra-pair paternity rates in Swainson's Hawks (*Buteo swainsoni*), as their gregarious nature during the migratory and non-breeding seasons, and relatively high nesting densities in our study area may facilitate greater levels of extra-pair paternity. We examined extra-pair paternity rates in 56 offspring from 19 unique pairs and 27 nesting attempts from 2008-2010. We found evidence of extra-pair paternity in 5% of offspring and 7% of nesting attempts. These relatively low extra-pair paternity rates were not related to nesting density (i.e., the average distance of the three nearest neighbors), are typical of raptors, and may help demonstrate that despite relatively high densities, mechanisms to limit extra-pair paternity (e.g., sperm competition) may generally be sufficient to prevent extra-pair fertilization.

Key words: *Buteo swainsoni*, *density*, *extra-pair fertilization*

Introduction

Advances in molecular techniques have demonstrated that species once thought to be monogamous may have high rates of extra-pair paternity (EPP, Griffith et al. 2002). In birds, the Passeriformes have generally shown high rates of EPP that can exceed 50% of offspring produced (e.g., Dixon et al. 1994, Morton et al. 1998). In contrast, non-Passeriformes have generally exhibited relatively low rates of EPP, generally on the order of 0-10% of offspring produced (reviewed in Griffith et al. 2002). In species that have been examined, raptors (i.e., Accipitriformes, Falconiformes and Strigiformes) are typical of non-Passeriformes birds with low EPP rates (e.g., Gavin et al. 1998, Villarroel et al. 1998, Rudnick et al. 2005). However, few studies have used genetic techniques to examine EPP in raptorial species, which generally produces better estimates of EPP (Griffith et al. 2002).

As males of most raptorial species have high levels of parental care (Newton 1979), they may have developed mechanisms to ensure decreased extra-pair copulations (EPCs) and subsequent EPP (Møller 1987, Birkhead and Møller 1992). As a consequence, these mechanisms should increase an individual's fitness by limiting the energetically expensive activity of rearing a rival's offspring. Several factors have been implicated in maintaining these low rates. For example, territoriality and high copulation frequency while the female is fertile may result in resident males swamping sperm from competitors even if extra-pair copulations occur (Møller 1987, Mougeot 2004). Alternatively, factors such as high nesting density may increase the opportunities for EPCs and subsequent EPP within a species (Westneat and Sherman 1997). In fact,

nesting density has been implicated as a factor in EPP rates in several species (e.g., Gibbs et al. 1990, Charmantier and Perret 2004).

Swainson's Hawks (*Buteo swainsoni*) are highly gregarious during the wintering season and throughout migration, forming flocks that can be in the tens of thousands of individuals (Jaramillo 1993). This sociality, if still tolerated in the breeding season, could lead to increased opportunities for EPCs and EPP. However, during the breeding season (i.e., April – August), breeding pairs are highly territorial against both inter- and intraspecific competitors (Rothfels and Lein 1983, England et al. 1997), which could limit the opportunities for EPP. While Swainson's Hawks are generally socially monogamous, there have been observations of EPCs and polyandry (B. Woodbridge pers. comm.); however, nothing is known about EPP rates. Therefore, we examined rates of EPP in Swainson's Hawks between nests and amongst offspring. If nesting density and gregarious behavior in other parts of the annual cycle influence EPP rates, then male Swainson's Hawks may be cuckolded more frequently than other raptor species.

Methods

We monitored a breeding population of Swainson's Hawks from 1979-2010 in Butte Valley, CA. Breeding adults were trapped with a Great-horned Owl (*Bubo virginianus*) and dho-gaza style net (Bloom et al. 1992) or bal-chatri baited with a mouse (Berger and Mueller 1959). Once trapped, we gave adults unique alpha-numeric color bands for individual identification. Nestlings were banded using USGS aluminum bands when they reached at least 3 weeks of age. From 2008-2010 we collected and stored blood samples from breeding adults and nestlings in heparinized tubes. Blood was kept

on ice for < 3 hours and then spun at >6000rpm for 10 minutes and the plasma was separated from the red blood cells. We restricted the analysis to nests where we had blood samples from both defending adults to assess scoring error rates by examining the relationship between mother and offspring, as we are not aware of incidents of brood parasitism in *Buteos*.

We extracted DNA from whole red blood cells using Qiagen DNEasy kits following manufacturer protocols for blood extraction. Each DNA extraction was quantified using a Labsystems Fluoroskan Ascent flurometer. We used a total of 9 microsatellite loci developed for Swainson's Hawks developed by Hull et al. (2007). Specifically, we used BswA312w, BswD237w, BswD234w, BswA204w, BswD107w, BswD127w, BswD324w, BswD223w, and BswA303w (Hull et al. 2007). Primers for each locus had one of three M13 labels according to Schuelke (2000). All forward primers had one of three M13 tails corresponding with the label NED, VIC or FAM attached to the 5' end. We also added GTTTCTTT to the 5' end to reduce drive the non-template addition of a base onto the 3' end of the labeled strands. We used multiplex (3 microsatellite primer pairs) polymerase chain reaction (PCR) for each loci.

A multiplex primer cocktail was prepared to give a final primer concentration of 0.05 μ m of each tailed forward primer, 0.15 μ m of each reverse primer, and 0.1 μ m of each M13 fluorescently labeled primer in a 16 μ L reaction. Eight microliters of Multiplex *Taq* (QIAGEN) and approximately 50ng of template DNA were used. PCR parameters included a 15-min hot start at 95°C, followed by 41 cycles of 95°C for 30s, touchdown annealing temperature for 90s, and 72°C for 30s. The annealing temperatures for each

stage of the touchdown PCR were 65°C for 7 cycles, 61°C for 7 cycles, 58°C for 7 cycles, and 20 cycles at 55°C in which the first 21 cycles amplify the specific primer and the final 20 cycles add the fluorescently labeled M13 tail to the PCR product. However, BswA303w did not amplify under the above conditions and was excluded from all analyses, leaving 8 microsatellite loci.

All PCR was carried out on a MBS Satellite 0.2G thermal cycler in 16µl volumes. PCR product was diluted to proper intensity and 1µl was added to 19µl of GeneScan 500 LIZ size standard with Hi-Dye Formamide (Applied Biosystems). Fragment analysis was carried out on an Applied Biosystems (ABI) Prism 3730 DNA Analyzer. All alleles generated were scored, binned, and given allelic and genotypic designation using ABI GeneMapper software (version 3.7).

We used Cervus 3.0 (Kalinowski et al. 2007) to estimate paternity in birds to account for missing alleles, null alleles, mutations, and genotyping errors. We examined the frequency of heterozygotes of all markers, calculated differences from Hardy-Weinberg equilibrium, and estimated null allele frequency. Using our microsatellite markers we calculated the non-exclusion probability at <0.001 for individuals that were scored for all 8 loci. We calculated LOD scores for each nestling, which is the natural logarithm of the ratio of the putative father being the true father compared to a randomly selected male from the population. Thus, individuals with positive LOD scores are likely to be the father and those with negative LOD scores are unlikely to be the father. We calculated the LOD score necessary to be at least 95% confident that proposed father was

the true genetic father. Nestlings below the 95% confidence limit for parentage analysis were considered the product of extra-pair fertilization.

We used the frequency of EPP calculated above to correlate instances of EPP with nesting density. To measure nesting density we calculated the average distance to the three nearest neighbors for each of the nest attempts examined. We used a t-test to determine if cuckolded males nested in areas with higher nest density, and therefore there was greater opportunity for EPCs.

Results

All alleles used in this analysis demonstrated Hardy-Weinberg equilibrium ($P > 0.4$ for all alleles). The LOD score that allowed >95% confidence in paternity assignment was -2.5. We examined 56 nestlings from 19 unique pairs and 27 nesting attempts. One female was observed nesting with separate males in consecutive years. We collected genetic samples from 2.0 ± 0.14 offspring per nesting attempt. Of the 56 nestlings we genotyped, 3 individuals (5%) from 2 nesting attempts (7%) were the product of EPP. LOD scores from all individuals demonstrated >95% confidence in assignment of paternity for all remaining individuals.

Swainson's Hawks in our study area nested at relatively high densities from 2008-2010, averaging one pair per $5.3 \pm 0.3 \text{ km}^2$. Nesting density, as assessed from average nearest neighbor distances, was not related to EPP rates in uncuckolded ($1770 \pm 136 \text{ m}$) versus cuckolded ($1157 \pm 159 \text{ m}$) nests ($t = 1.25$, $df = 25$, $P = 0.22$)

Discussion

Our results indicate that EPP rates in Swainson's Hawks are low; that is, 5% of chicks and 7% of nesting attempts. These results are comparable with what has been reported in other raptorial species (e.g., Villarroel et al. 1998, Arsenault et al. 2002, Rudnick et al. 2005). While Swainson's Hawks in this population have been observed engaging in polyandry (B. Woodbridge, pers. comm.), none of the pairs included in this analysis were known to be polyandrous. This polyandry is also exhibited, albeit more widely, in the only other species in the genus *Buteo* that has been examined, the Galapagos Hawk (*Buteo galapagoensis*). Galapagos Hawks also exhibit low rates of EPP when pairs are socially monogamous (Faaborg et al. 1995). However, an insular species with widely varying mating systems (Faaborg et al. 1995) may not be representative of *Buteo* species as a whole and further studies are needed to assess EPP rates in other raptor species to determine if rates observed in Swainson's Hawks are really typical.

Only two nests in our study exhibited EPP, one of which had two nestlings that were the result of EPC. A third nestling from that nest attempt was too small to band at the time the other nestlings were banded and died prior to us obtaining a genetic sample. The year following that attempt the cuckolded male was replaced; however, the replacement male was also not the genetic father of the offspring with >95% certainty. There was no significant difference in average distance to the three nearest neighbors between cuckolded and uncuckolded nests, indicating that nesting density may not play a role in EPP for Swainson's Hawks; however, as sample sizes of cuckolded males was small increasing our sample size may reveal nesting density is an important factor in EPP in Swainson's Hawks. As our study population is near average nesting density for its size

relative to other Swainson's Hawk studies (Smallwood 1995), it is reasonable to predict that this population may be representative of other studies. However, more work should focus on low-density nesting areas to get a more representative sample of the species across its range to better assess the effects of nesting density on RPP (Smallwood 1995)

EPP rates may be kept low by the aggressive nature of breeding Swainson's Hawks. Such aggression may limit the opportunities for EPCs to occur. Additionally, the relatively open landscape may allow ready detection of an intruding male, giving resident males the opportunity to further restrict EPC opportunities. These factors may help males maintain low EPP rates in Swainson's Hawks, despite relatively high nesting densities in this study area and highly social wintering behavior. As a consequence, mechanisms that minimize EPP rates in Swainson's Hawks may be generally sufficient to minimize investment in extra-pair offspring and maximize their own fitness.

Our primary method of capture (i.e. dho-gaza style net with a Great-horned Owl lure) may be biased, since the method only captures individuals aggressive enough to stoop on a Great-horned Owl lure. If we are biased towards more aggressive individuals in our sample of nesting pairs, we may underestimate EPP rates because aggressive males may be less tolerant and/or more vigilant of conspecifics. While none of the 3 males that were trapped using a bal-chtri, a method that does not rely on aggression to trap the individual, were cuckolded more information is needed to determine if there is a bias in trapping methodology. Despite this potential limitation, it is likely that EPP rates in Swainson's Hawks are consistent with other socially monogamous raptor species.

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Literature Cited

- ARSENAULT, D. P., P. B. STACEY and G. A. HOELZER. 2002. No extra-pair fertilization in Flammulated Owls despite aggregated nesting. *The Condor*, 104: 197-201.
- BERGER, D. D. and H. C. MUELLER. 1959. The bal-chatri: a trap for the birds of prey. *Bird-banding*, 30: 18-26.
- BIRKHEAD, T. R. and A. P. MØLLER. 1992. *Sperm Competition in Birds*, Academic Press, London.
- BLOOM, P. H., J. L. HENCKEL, E. H. HENCKEL, J. K. SCHMUTZ, B. WOODBRIDGE, J. R. BRYAN, R. L. ANDERSON, P. J. DETRICH and T. L. MAECHTLE. 1992. The dho-gaza with great horned owl lure: An analysis of its effectiveness in capturing raptors. *Journal of Raptor Research*, 26: 167-178.
- CHARMANTIER, A. and P. PERRET. 2004. Manipulation of nest-box density affects extra-pair paternity in a population of blue tits (*Parus caeruleus*). *Behavioral Ecology and Sociobiology*, 56: 360-365.
- DIXON, A., D. ROSS, S. L. C. O'MALLEY and T. BURKE. 1994. Paternal investment inversely related to degree of extra-pair paternity in the reed bunting. *Nature*, 371: 698-700.

- ENGLAND, A. S., M. J. BECHARD and C. S. HOUSTON (1997) Swainson's Hawk (*Buteo swainsoni*). In: *Birds of North America, No. 265* (POOLE, A. and GILL, F., eds.). The American Ornithologists' Union, Washington, D.C.
- FAABORG, J., P. PARKER, L. DELAY, T. VRIES, J. BEDNARZ, S. MARIA PAZ, J. NARANJO and T. WAITE. 1995. Confirmation of cooperative polyandry in the Galapagos hawk (*Buteo galapagoensis*). *Behavioral Ecology and Sociobiology*, 36: 83-90.
- GAVIN, T. A., R. T. REYNOLDS, S. M. JOY, D. LESLIE and B. MAY. 1998. Genetic evidence for low frequency of extra-pair fertilizations in Northern Goshawks. *The Condor*, 100: 556-560.
- GIBBS, H. L., P. J. WEATHERHEAD, P. T. BOAG, B. N. WHITE, L. M. TABAK and D. J. HOYSAK. 1990. Realized reproductive success of polygynous red-winged blackbirds revealed by DNA markers. *Science*, 250: 1394-1397.
- GRIFFITH, S. C., I. P. F. OWENS and K. A. THUMAN. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology*, 11: 2195-2212.
- HULL, J. M., D. TUFTS, J. R. TOPINKA, B. MAY and H. B. ERNEST. 2007. Development of 19 microsatellite loci for Swainson's hawks (*Buteo swainsoni*) and other buteos. *Molecular Ecology Notes*, 7: 346-349.
- JARAMILLO, A. P. 1993. Wintering Swainson's Hawks in Argentina: food and age segregation. *Condor*, 95: 475-479.
- KALINOWSKI, S. T., M. L. TAPER and T. C. MARSHALL. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology*, 16: 1099-1106.

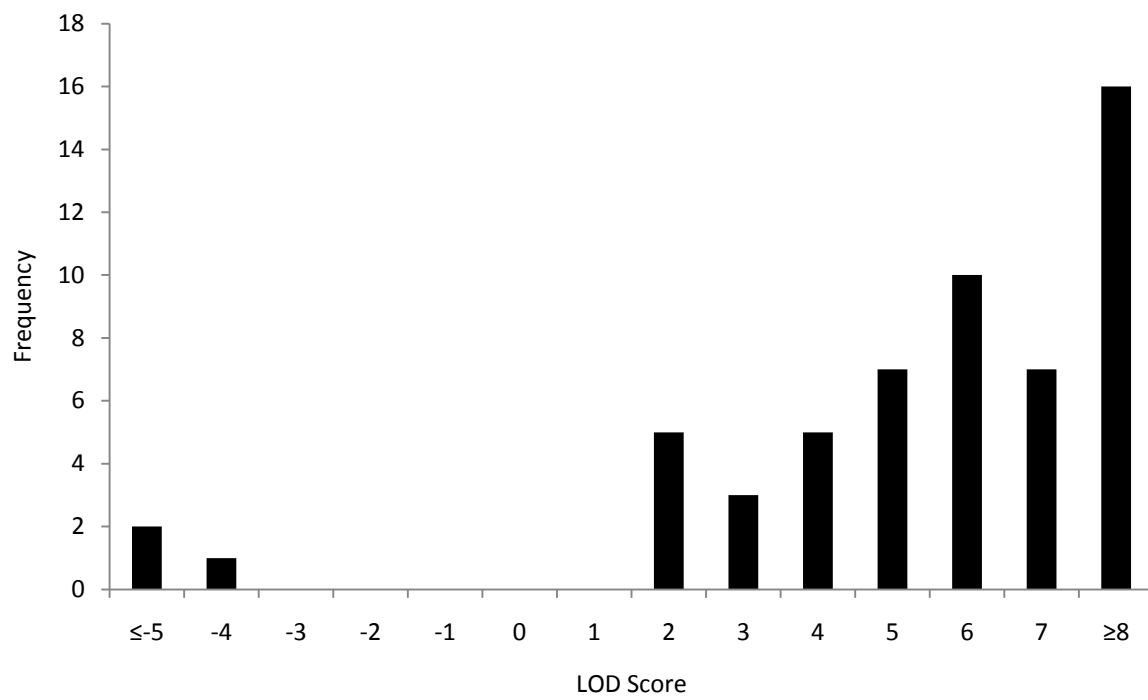
- MØLLER, A. P. 1987. Copulation behaviour in the goshawk, *Accipiter gentilis*. *Animal behaviour*, 35: 755-763.
- MORTON, E. S., B. J. M. STUTCHBURY, J. S. HOWLETT and W. H. PIPER. 1998. Genetic monogamy in blue-headed vireos and a comparison with a sympatric vireo with extrapair paternity. *Behavioral Ecology*, 9: 515-524.
- MOUGEOT, F. 2004. Breeding density, cuckoldry risk and copulation behaviour during the fertile period in raptors: a comparative analysis. *Animal behaviour*, 67: 1067-1076.
- NEWTON, I. 1979. *Population ecology of raptors*, Poyser, Berkhamstead.
- ROTHFELS, M. and M. R. LEIN. 1983. Territoriality in sympatric populations of red-tailed and Swainson's hawks. *Canadian Journal of Zoology*, 61: 60-64.
- RUDNICK, J. A., T. E. KATZNER, E. A. BRAGIN, O. E. RHODES JR and J. A. DEWOODY. 2005. Using naturally shed feathers for individual identification, genetic parentage analyses, and population monitoring in an endangered Eastern imperial eagle (*Aquila heliaca*) population from Kazakhstan. *Molecular Ecology*, 14: 2959-2967.
- SCHUELKE, M. 2000. An economic method for the fluorescent labeling of PCR fragments. *Nature Biotechnology*, 18: 233-234.
- SMALLWOOD, K. S. 1995. Scaling Swainson's hawk population density for assessing habitat use across an agricultural landscape. *Journal of Raptor Research*, 29: 172-178.

VILLARROEL, M., D. BIRD and U. KUHNLEIN. 1998. Copulatory behaviour and paternity in the American kestrel: the adaptive significance of frequent copulations. *Animal behaviour*, 56: 289-299.

WESTNEAT, D. F. and P. W. SHERMAN. 1997. Density and extra-pair fertilizations in birds: a comparative analysis. *Behavioral Ecology and Sociobiology*, 41: 205-215.

Figures

Figure 1 – Histogram of LOD scores for all offspring Swainson's Hawks genotyped in Butte Valley, CA. A LOD score of >1 indicated a $>95\%$ probability that the social father was also the genetic father. A LOD score of <-2.5 indicates that the social father was not the genetic father with $>95\%$ confidence.



Chapter 5 - Seasonal Interactions in Swainson's Hawks

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Abstract

Carry-over effects are how processes and events outside of the breeding season can influence reproduction. We examine the influence of carry-over effects on nest success and nest productivity of Swainson's Hawks (*Buteo swainsoni*) breeding in northern California from 2008-2010. We use feathers as a proxy of body condition of individuals. Specifically, we used the average daily growth of the feather, the level of corticosterone in the feather, and the number of fault bars in the retrices and remiges of breeding hawks. We used deuterium levels in feathers to determine where each feather was grown to ensure that indices of condition came from a known geographic location. Average daily growth was correlated with mass adjusted for body size, but corticosterone in feathers and fault bars were not. For males, average daily growth of feathers grown in Argentina and number of fault bars on worn feathers were correlated with nest success demonstrating carry-over effects and that individuals in good body condition on their wintering grounds had higher reproductive performance. In contrast, measures of feather condition in females were not correlated with nest success. Corticosterone in feathers was higher in breeding males, but not in females. As males are the primary providers of prey for both the female and young nestlings their condition may drive the ability of a nesting attempt to succeed because an individual in poor condition may not be able to effectively provision the female or offspring.

Introduction

Countless studies have examined factors associated with reproductive success, including age (Fowler 1995), weather (Wingfield 1984), and food availability (Arcese and Smith 1988). An issue that has garnered recent attention is the ability of events and conditions outside of the current breeding attempt to affect current reproductive output, or carry-over effects (Webster et al. 2002). For migratory species, processes and events in wintering areas and along the migratory route have often been correlated with poor reproductive performance (reviewed in Norris and Marra 2007, Harrison et al. 2011), but many studies have examined relative habitat quality of the assumed wintering areas using broad spatial tools (e.g., remotely sensed data across a wide geographic range, Gordo and Sanz 2008). However, the logistical challenges of following individuals throughout the annual cycle have made understanding carry-over effects at the individual level more difficult to determine (but see Norris et al. 2004).

Habitat quality (Studds and Marra 2005, Balbontin et al. 2009), food abundance, and density dependence (Runge and Marra 2005) on the wintering grounds have all been shown to have the potential to influence a population when subsequently on its breeding grounds (Norris 2005, Runge and Marra 2005, Balbontin et al. 2009), particularly its reproduction (Marra et al. 1998, Bearhop et al. 2004). These seasonal interactions can influence reproduction in a number of ways. Individuals in better condition on the wintering grounds can depart earlier (Marra and Holmes 2001), arrive on the breeding sites earlier, and acquire higher quality territories (Marra et al. 1998). Earlier onset of incubation has been linked with increased nest success (Klomp 1970) and offspring survival until breeding (Cooke et al. 1984), and could be a mediator in migratory species

with carry-over effects delaying migration in some species (reviewed in Harrison et al. 2011). Thus, individuals that are able to obtain higher quality sites or are more efficient at foraging may be better situated in the breeding season and be able to increase reproduction. Even slight differences in reproduction from year to year due to acquisition of a good territory or knowledge of good habitat in a wintering area could accrue large fitness benefits for long-lived species.

Because population growth (λ) is generally heavily reliant upon adult survival in long-lived species (Saether and Bakke 2000), selection may constrain adult survival towards its maximum value (Stearns 1992). In other words, given energetic limitations an individual should choose to support behaviors or physiology that increase its chances of survival over other activities such as reproduction. Therefore, external factors (e.g. limiting food supply) generally have more influence on reproduction (Stearns 1992). By changing conditions and management action, we are most effective in increasing λ by increasing reproduction. We can then expect that poor conditions (e.g. nutrition, habitat, etc.) would first be reflected in decreased reproduction rather than survival.

We propose to use feathers to examine how carry-over effects influence the reproduction of Swainson's hawks (*Buteo swainsoni*), a long-lived hawk that breeds throughout western North America and winters primarily in the pampas (i.e. grasslands) of Argentina. Feathers are metabolically inert once grown and retain chemical and isotopic signatures of the period when they were grown (Hobson and Wassenaar 1996). Additionally, Swainson's Hawks frequently molt both on the breeding grounds (Schmutz 1992) and on their wintering grounds (Bechard and Weidensaul 2005), which provides us the opportunity to examine feathers molted in both areas. Previous work on Swainson's

hawks has shown that pesticide induced mass-mortality events on their wintering grounds (Woodbridge et al. 1995, Goldstein et al. 1996, Goldstein et al. 1999) influenced the population dynamics of individuals breeding in California (Briggs et al., in revision). However, it is unknown if Swainson's hawks could also suffer sub-lethal effects (i.e., carry-over effects) from conditions or events in Argentina. Feathers can provide information on body condition in several ways; ptilochronology, fault bars, and corticosterone (CORT).

Ptilochronology examines averaging daily growth of feathers by examining the patterns of light and dark areas of feathers. Average daily growth of feathers has been shown to be a reasonable index of condition in a number of species (reviewed in Grubb 1995). When an individual is in good condition (i.e. has ample energetic reserves), it can convert those reserves to increased feather growth and the average length of a daily growth bar increases. Fault bars are an extension of daily growth bars and occur when an individual is in such poor condition that there was a lack of resources to sufficiently create feather for that time period, leaving a line of missing barbules through the feather perpendicular to the rachis (Murphy et al. 1989). The occurrence of fault bars has been correlated with survival and breeding probability (Bortolotti et al. 2002).

CORT is a glucocorticoid that is related to stress and regulation of foraging behavior. Short term increases in CORT help the mobilization of resources and may increase the likelihood of foraging (Astheimer et al. 1992, Holberton 1999). However, prolonged high levels of CORT can have deleterious effects if elevated for long periods; these effects include depression of immune function (Sapolsky et al. 2000), catabolization of protein (Holmes and Phillips 1976), and decreased offspring production

(Saino et al. 2005). Circulating CORT can be deposited in feathers during feather growth and can provide an index of stress around the time the feather was grown (Bortolotti et al. 2008). High CORT in feathers are well correlated with times of high stress (Bortolotti et al. 2008). Additionally, CORT has been hypothesized to be correlated with nest success, but in practice, this relationship is not always observed (reviewed in Breuner et al. 2008, Bonier et al. 2009).

We predict that measures of feather condition (i.e., CORT, average daily growth, and fault bars) will be correlated with traditional measures of body condition (i.e., mass adjusted for body size, Brown 1996). These long-term measures of condition will then be correlated with nest success, as carry-over effects from processes and events in Argentina will influence nest success and nest productivity of breeding individuals. In addition, feathers from breeding individuals will have higher CORT levels, with a greater number of offspring increasing CORT levels and decreasing average daily growth of the feathers.

Methods

We monitored a population of Swainson's Hawks in the Butte Valley, California from 2008-2010. Adults were individually color marked using unique 2-digit color bands and a US Geological Survey (USGS) aluminum band. Adults were trapped using dho-gaza style net with a great-horned owl lure (*Bubo virginianus*, Bloom et al. 1992) or a bal-charti baited with mice (Berger and Mueller 1959). Trapped adults were photographed opportunistically with one wing open to document plumage. Sex was determined by examining individuals for a brood patch, by size measurements, and by observing copulatory behavior.

Territories were monitored annually and nest sites were located by watching for nest building, mating behavior, and territoriality (April – May). In the summer months, nests were found by watching for prey deliveries to the nest site. The nest tree was climbed approximately two weeks after the mean hatch date to determine nesting status and determine chick age. Nestlings were banded with standard USGS aluminum bands approximately 1-2 weeks before fledging.

We also trapped individuals wintering in the province of La Pampa, Argentina using a bal-chatri trap. For all individuals trapped in either California or La Pampa we measured unflattened wing chord and weight. We also collected freshly molted secondary coverts from each individual we trapped and collected a feather that was molting in whenever one was available. We documented the location of fault bars on all flight feathers (i.e., retrices and remiges, Newton 1986, Machmer et al. 1992) and documented if the feather was showed little or no signs of wear (i.e. new) or showed signs of significant wear (i.e. old). Newly-grown feathers can generally be discerned by a lack of wear or fading.

Body condition was measured by using a standard major axis (SMA) regression to predict body condition (Peig and Green 2009). We regressed the natural log of weight against the natural log of wing chord. We obtained a measure of condition by subtracting the predicted condition of the SMA regression from actual condition. The difference between the actual weight of the individual and the predicted weight was considered the condition. We separately calculated condition for males and females.

Feather Measures of Condition

We measured the ptilochronology of the new feather following Grubb (1989b) by taping the feather to an index card and using a pin to mark locations of each daily growth bar for the first 30-50mm of the feather. We divided the length of the feather we measured by the number of growth bars to get the average daily growth of the feather.

We measured the amount of CORT in the first 50mm of feathers collected in 2010 and select feathers from 2008-2009 from breeding individuals. We followed Bortolotti et al. (2008) in our extraction procedure, with the exception that the CORT was resuspended in 250 μ L of assay buffer 15 (Enzo LifeSciences) instead of phosphate buffer system. We measured total concentration of CORT using an enzyme immunoassay (EIA) kit (Enzo LifeSciences, Breuner and Orchinik 2002, Love et al. 2004). EIA sensitivity was 32-20,000 pg/well and was fit with a four-parameter logistic fit. All observations fell within this range. All samples were run in duplicate to determine inter- and intra-assay variation (7.3% and 8.7%, respectively).

We examined deuterium concentration (δ D) of each feather to determine where a feather was molted. We could compare these values with individuals whose δ D are known (i.e. feathers that were molting). We washed each feather to remove oils following Paritte and Kelly (2009), and analyzed each feather at the Nevada Stable Isotope Laboratory in Reno, Nevada, as described in Wassenaar and Hobson (2003). As δ D signatures varied greatly between Butte Valley, California and the pampas of Argentina (Bowen et al. 2005), we could determine if a given feather was grown during the wintering period (i.e., in the pampas of Argentina) or on the breeding grounds. We used feathers that were still in sheath in both Butte Valley, California and Argentina to determine mean δ D for each area to ensure the accuracy of our assignment of locations.

Nest Success

We examined reproduction through analysis of both nest survival and nest productivity. Nest survival was defined by whether a nesting attempt failed (i.e., produced no fledglings) or succeeded (i.e., produced at least one fledgling). We quantified daily nest survival using hierarchical Bayesian daily nest survival models (Schmidt et al. 2010) that calculated potential differences between individuals with different wintering condition in nest survival using the R package “R2WinBUGS” (Sturtz et al. 2005) in R 2.10.1 and WinBUGS 1.4.3 (Lunn et al. 2000). These models account for biases in apparent nest survival, due to the potential to miss nests after they have failed, by accounting for nest detection probability (Mayfield 1961, 1975). They also account for potential problems with pseudoreplication of monitoring the same nest sites over multiple years (Hurlbert 1984). Using these models, we examined the influence of condition of attendant males and females that we caught using both feather measures as well as the residuals from our SMA regression. All covariates were standardized to a mean of 0 and standard deviation of 1.

Convergence of the Markov chain Monte Carlo (MCMC) runs was assessed using the Rafert-Lewis and Gelman-Rubin diagnostic tests in the R package “coda” (Gelman and Rubin 1992, Plummer et al. 2006). We used a reversible jump Monte Chain Monte Carlo (RJMCMC) method through the WinBUGS JUMP interface (Spiegelhalter et al. 2002, Lunn et al. 2009). RJMCMC was used to assess the performance of covariates using the posterior probability (Green 1995), and covariates with a high marginal posterior probability (i.e., >0.85) were considered influential. We used flat, or uninformative, priors so that each model had an equal likelihood *a priori*, with 200,000

iterations, discarding the first 15,000 as burn-in to ensure complete mixing. A RJMCMC allows the model to move through parameter space, selecting covariates if they aid in model fit. At each step of the MCMC the parameter values in the model are updated. Thus, for each step we can determine parameter values and which parameters have been selected. At the end of the modeling, the amount of time spent in a given model (i.e. the marginal posterior probability) indicates the relative support for that model. Cumulative statistics of parameters of interest (e.g., mode, credible intervals) can then be extracted using MCMC that account for model uncertainty (King and Brooks 2004).

Nest Productivity

We also examined the potential impacts of conditions in Argentina on the number of offspring produced (i.e., nest productivity). For nests that successfully reproduced offspring we used the lme4 package (Bates and Maechler 2009) in R 2.10.1 (R Development Core Team 2009) and a Poisson distribution to regress the average daily growth of feathers, number of fault bars observed in worn feathers, and amount of CORT in feathers grown in Argentina against the number of offspring fledged. We used year and territory as random factors in the analysis. Additionally we used average daily growth and CORT of growing feathers as well as number of fault bars in feathers with little or no wear. We used each variable iteratively for males and females separately to investigate differences in relationship between our indices of condition and number of fledglings produced. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to assess model fit (Akaike 1973, Burnham and Anderson 2002). Models >2

AIC_c units from the best model are generally considered uncompetitive, and we used model weights to evaluate evidence for each term.

Nest Timing

We used generalized linear models to investigate the correlation of our feather indices with nest timing. We regressed our feather measures from both Argentina and the nesting area against Julian date of the beginning of nest timing, where the earliest nest date of the year was set to 1. Again, we analyzed males and females separately and used AIC_c and model weights to assess model fit.

Results

Feather Measures of Condition

We trapped 101 (56 male, 45 female) breeding individuals in and around Butte Valley, California from 2008-2010. In addition, we trapped 33 individuals while on their wintering grounds in Argentina in Jan 2010. We collected feathers that were freshly molting from individuals; 22 breeding in and around Butte Valley, California and 9 wintering individuals in La Pampa, Argentina. Molting feathers from breeding individuals ranged from -7 to -48 δ D, and molting feathers from individuals trapped in Argentina ranged from -71 to -108 δ D. Any feather with a δ D measure outside of this range was excluded from further analysis because the origin of the feather was unknown. Of the feathers that were collected from breeding individuals, 73% of the individuals were correctly classified as from Argentina (i.e., worn and faded feathers classified as old were from Argentina) and 86% were correctly classified as grown in or around Butte Valley, based on the known values.

Body condition, as measured from SMA regression, was significantly correlated with average daily growth of feathers that were molting ($P=0.01$, $n=31$), but not correlated with CORT level in the feathers grown in the same season ($P=0.15$, $n=21$, Table 1). Feather CORT was not correlated with feather weight ($P=0.65$, $n=189$), average daily growth of the feather ($P=0.58$), or number of fault bars.

Nest success

For females, the probability that a nest produced at least one offspring was not correlated with any of our measures of condition from feathers grown in Argentina ($n = 32$) or on their breeding grounds ($n = 35$). In contrast, among males, 3 measures of feather condition had >0.85 marginal probability (Table 2). First, the number of fault bars recorded in worn feathers and the average daily growth of feathers in Argentina was negatively correlated with nest success ($n = 28$; Table 2; however, we could not determine where each feather listed as old or new was grown and this measure likely encompasses a time period that extends beyond just the wintering grounds. A 1 SD increase in the number of fault bars decreased seasonal nest survival by 7.3%.

The average daily growth of a feather grown in Argentina was positively correlated with nest success for male Swainson's Hawks. With each 1 SD increase in daily growth in Argentina, seasonal nest success increased 3.0%.

Additionally, in males the amount of CORT in feathers grown while on the breeding grounds during that nest attempt was positively correlated with nest success ($n = 34$). However, other feather variables were unrelated to nest success. With each 1 SD increase in CORT in feathers, seasonal nest success increased 9.2%.

Nest productivity

None of our feather measures were correlated with number of fledglings produced in successful nests for either breeding males ($n = 36$) or breeding females ($n = 35$; Table 3), as demonstrated by no significant drop in AIC_c values for any of the covariates we used.

Nest timing

We found no relationship between nest timing and our feather measures either on the breeding grounds or from feathers grown in Argentina as the null model received the lowest AIC_c score (Table 4).

Discussion

Using feathers as indices of individual condition may provide longer-term and more integrated metrics compared to the more traditional snapshot of size-weight residuals (Grubb 1995, Bortolotti et al. 2008). Prior condition of males, as judged by fault bars on feathers that demonstrated signs of wear, was negatively correlated with nesting success, indicating that prior nutritional stress lowered an individual's nesting success. While we could not judge where each flight feather was grown, we had high success in ascribing feather location based on amount of wear, and therefore most of the data collected on fault bars from flight feathers was accurately described. By examining all flight feathers on an individual, we accounted for a longer temporal scale that cannot be matched by examining a single covert grown over the course of a few weeks. Similarly, the average daily growth of feathers in Argentina was positively correlated

with nest success. Therefore, an individual's condition over even a relatively small time frame of 2-3 weeks in Argentina was predictive of future nest success. By demonstrating that feather indices from Argentina were correlated with daily nest survival we show that carry-over effects can influence population dynamics recorded on the breeding grounds in northern California, approximately 10,000km away.

Processes and events in Argentina had a significant influence on the nest success of Swainson's hawks, demonstrating a seasonal interaction. However, it is unclear why individuals were in poor condition or how body condition in Argentina influences daily nest survival, given that there was not a difference in onset of incubation based on those measures. However, other factors, such as arrival on the breeding grounds, should be investigated as they have been shown to also play an important role in nest success in other species (Møller 1994).

Other studies have demonstrated that density dependence and food limitation can limit individual condition (Brown and Sherry 2006) and lowered condition outside the breeding grounds can influence population dynamics (Runge and Marra 2005, Norris and Taylor 2006). For example, in the American Redstart (*Setophaga ruticilla*) food availability on the wintering grounds is related to departure timing, arrival timing, and subsequent nest success (Marra et al. 1998). It is unclear if the limitation on condition for wintering Swainson's hawks was food, but the vagile nature on the wintering grounds (Canavelli et al. 2003) of this species and its gregarious nature provides them the opportunity locate resources and may limit density dependence. Thus, individuals may be more limited by their ability to locate and effectively capture prey. We could not use δD values to determine wintering location because of the low variability in δD

throughout the pampas of Argentina. Also, the wide variability of our δD values for Butte Valley, where the location of the molting feather was known, was wider than expected based on the small geographic area and could indicate an inability to accurately describe an area a feather was molted based solely on δD values.

In contrast to prior breeding condition, successfully reproducing males had higher feather CORT measures, indicating that successfully reproducing individuals may have higher stress levels. Previous studies have indicated that higher stress, and the concomitant increased chronic CORT increases, could impact future survival (reviewed in Bonier et al. 2009). Because Swainson's Hawks are a long-lived species, we expect that production of offspring should lead to minimal or no increases in stress to maximizing survival and subsequent reproductive value. Individuals in long-lived species that maximize adult survival are able to increase the number of future reproduction attempts and have the potential to greatly increase fitness, compared to individuals that trade-off future adult survival in favor of reproduction (Williams 1966, Stearns 1992).

In contrast to males, individual condition, as judged by feather measurements was not a reasonable predictor of nest success in females. This contrasts the idea that female condition and CORT levels can impact nest success (D'Alba et al. 2011). As males are the primary prey providers for females on eggs and young nestlings, the success of a nesting attempt relies on a male's ability to provision its offspring (Fitzner 1980). Therefore when nests are successful, males may have increased stress as they provision their mates of offspring with prey. Increased circulating CORT levels have been documented with increased reproductive effort in a number of species (e.g., Silverin and

Wingfield 1982, Kitaysky et al. 1999). In contrast, when nests have failed males no longer have to provision a mate and nestlings, reducing their workload and potential stress. Alternatively, higher CORT levels may be adaptive in some situations (Sinervo and DeNardo 1996). Higher CORT levels in breeding male Swainson's hawks may prompt individuals to increase foraging which may increase provisioning to offspring.

Feather CORT was not well correlated with individual condition or metrics of reproductive performance for freshly molting feathers, indicating the relationship between feather CORT and more transitional measures of condition may be more complicated than using average daily growth of feathers. Individuals in poor nutritive condition may have higher CORT levels, and thus circulating CORT levels may be a reasonable metric of individual condition. A number of factors could cause a breakdown in the utility of feather CORT as an accurate measure of condition. First, it is unknown how stressful events (e.g., predator chases) are averaged out with baseline CORT. Thus, a few stressful events over the course of several weeks may increase our estimate of time-integrated CORT found in feathers but have little influence on nest success. Similarly, naturally higher baseline CORT levels, without knowing what the stress-induced CORT levels are, may provide more limited insight into individual condition.

Neither our feather metrics nor individual body condition were reasonable predictors of how many offspring were produced for successful nests or for nest timing. There also was no additional increase in feather CORT measures among successful males as the number of feedings increased. Therefore males may limit their increase in stress due to successful reproduction, and its potentially adverse effects on body condition.

After this limited increase males may allow siblicide to dictate the number of offspring produced based on the amount of prey they can provide.

Carry-over effects may be common in migratory species, but relatively few studies have explicitly identified their effects. This study demonstrates that condition on the wintering grounds, even at a relatively small temporal scale (e.g., 2-3 weeks) may provide enough insight to predict nest success and demonstrate how carry-over effects can influence population dynamics in this species. Future work should focus on determining how processes and events on the breeding grounds subsequently interact with those on the wintering grounds to determine if individuals become trapped in a cycle of poor condition (Harrison et al. 2011).

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Literature Cited

Akaike, H. 1973. Information Theory as an extension of the maximum likelihood principle. Pages 267-281 *in* B. N. Petrov and F. Csaki, editors. Second international symposium on Information Theory. Akademiai, Kaido.

- Arcese, P. and J. N. M. Smith. 1988. Effects of population density and supplemental food on reproduction in song sparrows. *The Journal of Animal Ecology*:119-136.
- Astheimer, L. B., W. A. Buttemer, and J. C. Wingfield. 1992. Interactions of corticosterone with feeding, activity and metabolism in passerine birds. *Ornis Scandinavica*:355-365.
- Balbontin, J., A. P. Moller, I. G. Hermosell, A. Marzal, M. Reviriego, and F. de Lope. 2009. Individual responses in spring arrival date to ecological conditions during winter and migration in a migratory bird. *Journal of Animal Ecology* **78**:981-989.
- Bates, D. and M. Maechler. 2009. lme4: Linear mixed-effects models using S4 classes. R package version 0.99375-32.
- Bearhop, S., G. M. Hilton, S. C. Votier, and S. Waldron. 2004. Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. *Proceedings of the Royal Society Biological Sciences Series B* **271**:S215-S218.
- Bechard, M. J. and C. S. Weidensaul. 2005. Feather molt by Swainson's hawks (*Buteo swainsoni*) on the austral grounds of Argentina. *Ornitologia Neotropical* **16**:267-270.
- Berger, D. D. and H. C. Mueller. 1959. The bal-chatri trap: a trap for the birds of prey. *Bird-banding* **30**:18-26.

- Bloom, P. H., J. L. Henckel, E. H. Henckel, J. K. Schmutz, B. Woodbridge, J. R. Bryan, R. L. Anderson, P. J. Detrich, and T. L. Maechtle. 1992. The dho-gaza with great horned owl lure: An analysis of its effectiveness in capturing raptors. *Journal of Raptor Research* **26**:167-178.
- Bonier, F., P. R. Martin, I. T. Moore, and J. C. Wingfield. 2009. Do baseline glucocorticoids predict fitness? *Trends in Ecology & Evolution* **24**:634-642.
- Bortolotti, G., T. Marchant, J. Blas, and T. German. 2008. Corticosterone in feathers is a long term, integrated measure of avian stress physiology. *Functional Ecology* **22**:494-500.
- Bortolotti, G. R., R. D. Dawson, and G. L. Murza. 2002. Stress during feather development predicts fitness potential. *Journal of Animal Ecology* **71**:333-342.
- Bowen, G. J., D. A. Winter, H. J. Spero, R. A. Zierenberg, M. D. Reeder, T. E. Cerling, and J. R. Ehleringer. 2005. Stable hydrogen and oxygen isotope ratios of bottled waters of the world. *Rapid communications in mass spectrometry* **19**:3442-3450.
- Breuner, C. and M. Orchinik. 2002. Plasma binding proteins as mediators of corticosteroid action in vertebrates. *Journal of Endocrinology* **175**:99.
- Breuner, C. W., S. H. Patterson, and T. P. Hahn. 2008. In search of relationships between the acute adrenocortical response and fitness. *General and Comparative Endocrinology* **157**:288-295.

- Brown, D. R. and T. W. Sherry. 2006. Food supply controls the body condition of a migrant bird wintering in the tropics. *Oecologia (Berlin)* **149**:22-32.
- Brown, M. E. 1996. Assessing body condition in birds. Pages 67-135 *in* V. Nolan and E.D. Ketterson, editors. *Current Ornithology*. Plenum Press, New York, New York, USA.
- Burnham, K. P. and D. R. Anderson. 2002. *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York, New York.
- Canavelli, S. B., M. J. Bechard, B. Woodbridge, M. N. Kochert, J. J. Maceda, and M. E. Zaccagnini. 2003. Habitat use by Swainson's Hawks on their austral wintering grounds in Argentina. *Journal of Raptor Research* **37**:125-134.
- Cooke, F., C. S. Findlay, and R. F. Rockwell. 1984. Recruitment and the timing of reproduction in Lesser Snow Geese (*Chen caerulescens caerulescens*). *The Auk* **101**:451-458.
- D'Alba, L., K. Spencer, R. Nager, and P. Monaghan. 2011. State dependent effects of elevated hormone: Nest site quality, corticosterone levels and reproductive performance in the common eider. *General and comparative endocrinology* doi:10.1016/j.ygcen.2011.03.006
- Fitzner, R. E. 1980. Behavioral ecology of the Swainson's Hawk (*Buteo swainsoni*) in Washington. Pac. NW Lab.

- Fowler, G. S. 1995. Stages of age-related reproductive success in birds: Simultaneous effects of age, pair-bond duration and reproductive experience. *American Zoologist* **35**:318-328.
- Gelman, A. and D. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* **7**:457-511.
- Goldstein, M. I., T. E. Lacher, Jr., B. Woodbridge, M. J. Bechard, S. B. Canavelli, M. E. Zaccagnini, G. P. Cobb, E. J. Scollon, R. Tribolet, and M. J. Hooper. 1999. Monocrotophos-induced mass mortality of Swainson's hawks in Argentina, 1995-96. *Ecotoxicology* **8**:201-214.
- Goldstein, M. I., B. Woodbridge, M. E. Zaccagnini, S. B. Canavelli, and A. Lanusse. 1996. An assessment of mortality of Swainson's hawks on wintering grounds in Argentina. *Journal of Raptor Research* **30**:106-107.
- Gordo, O. and J. J. Sanz. 2008. The relative importance of conditions in wintering and passage areas on spring arrival dates: the case of long-distance Iberian migrants. *Journal of Ornithology* **149**:199-210.
- Green, P. J. 1995. Reversible jump Markov chain Monte Carlo computation and Bayesian model determination. *Biometrika* **82**:711.
- Grubb, T. C. 1989. Ptilochronology - Feather growth bars as indicators of nutritional status. *Auk* **106**:314-320.

- Grubb, T. C. 1995. Ptilochronology: a review and prospectus. *Current ornithology* **12**:89-114.
- Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* **80**:4-18.
- Hobson, K. A. and L. I. Wassenaar. 1996. Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia* **109**:142-148.
- Holberton, R. L. 1999. Changes in patterns of corticosterone secretion concurrent with migratory fattening in a Neotropical migratory bird. *General and comparative endocrinology* **116**:49-58.
- Holmes, W. N. and J. G. Phillips. 1976. The adrenal cortex in birds. Pages 293-420 *in* I. Chester-Jones and I. Henderson, editors. *General and comparative endocrinology of the adrenal cortex*. Academic Press, New York.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological monographs* **54**:187-211.
- King, R. and S. P. Brooks. 2004. A classical study of catch-effort models for Hector's dolphins. *Journal of the American Statistical Association* **99**:325-333.

- Kitaysky, A., J. Wingfield, and J. Piatt. 1999. Dynamics of food availability, body condition and physiological stress response in breeding black legged kittiwakes. *Functional Ecology* **13**:577-584.
- Klomp, H. 1970. The determination of clutch-size in birds: a review. *Ardea* **58**:1-124.
- Love, O. P., C. W. Breuner, F. Vézina, and T. D. Williams. 2004. Mediation of a corticosterone-induced reproductive conflict. *Hormones and Behavior* **46**:59-65.
- Lunn, D. J., N. Best, and J. Whittaker. 2009. Generic reversible jump MCMC using graphical models. *Statistics and COmputing* **19**:395-408.
- Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS - a Bayesian modelling framework: concepts, structure, and extensibility. *Statistics and COmputing* **10**:325-337.
- Machmer, M. M., H. Esselink, C. Steeger, and R. Ydenberg. 1992. The occurrence of fault bars in the plumage of nestling ospreys. *Ardea* **80**:261-272.
- Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science (Washington D C)* **282**:1884-1886.
- Marra, P. P. and R. T. Holmes. 2001. Consequences of dominance-mediated habitat segregation in American redstarts during the nonbreeding season. *Auk* **118**:92-104.

- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* **73**:255-261.
- Mayfield, H. 1975. Suggestions for calculating nest success. *Wilson Bulletin* **87**:456-466.
- Møller, A. P. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. *Behavioral Ecology and Sociobiology* **35**:115-122.
- Murphy, M. E., B. T. Miller, and J. R. King. 1989. A structural comparison of fault bars with feather defects known to be nutritionally induced. *Canadian Journal of Zoology* **67**:1311-1317.
- Newton, I. 1986. *The Sparrowhawk*. T & A.D. Poyser Ltd., Calton.
- Norris, D. R. 2005. Carry-over effects and habitat quality in migratory populations. *Oikos* **109**:178-186.
- Norris, D. R. and P. P. Marra. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor* **109**:535-547.
- Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry, and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society Biological Sciences Series B* **271**:59-64.
- Norris, D. R. and C. M. Taylor. 2006. Predicting the consequences of carry-over effects for migratory populations. *Biology Letters* **2**:148-151.

- Paritte, J. M. and J. F. Kelly. 2009. Effect of cleaning regime on stable-isotope ratios of feathers in Japanese quail (*Coturnix japonica*). *The Auk* **126**:165-174.
- Peig, J. and A. J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* **118**:1883-1891.
- Plummer, M., N. Best, K. Cowles, and K. Vines. 2006. CODA: convergence diagnostics and output analysis for MCMC. *R News* **6**:7-11.
- Runge, M. C. and P. P. Marra. 2005. Modelling seasonal interactions in the population dynamics of migratory birds. Pages 375-389 *in* R. Greenberg and P. P. Marra, editors. *Birds of two worlds: the ecology and evolution of the temperate-tropical migration systems*. Johns Hopkins University Press, Baltimore, MD.
- Saether, B.-E. and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* (Washington D C) **81**:642-653.
- Saino, N., M. Romano, R. P. Ferrari, R. Martinelli, and A. P. Møller. 2005. Stressed mothers lay eggs with high corticosterone levels which produce low quality offspring. *Journal of Experimental Zoology Part A: Comparative Experimental Biology* **303**:998-1006.
- Sapolsky, R. M., L. M. Romero, and A. U. Munck. 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews* **21**:55.

- Schmidt, J. H., J. A. Walker, M. S. Lindberg, D. S. Johnson, and S. E. Stephens. 2010. A General Bayesian Hierarchical Model for Estimating Survival of Nests and Young. *The Auk* **127**:379-386.
- Schmutz, J. 1992. Molt of flight feathers in Ferruginous and Swainson's hawks. *Journal of Raptor Research* **26**:124-135.
- Silverin, B. and J. C. Wingfield. 1982. Patterns of breeding behaviour and plasma levels of hormones in a free living population of pied flycatchers, *Ficedula hypoleuca*. *Journal of Zoology* **198**:117-129.
- Sinervo, B. and D. F. DeNardo. 1996. Costs of reproduction in the wild: path analysis of natural selection and experimental tests of causation. *Evolution* **50**:1299-1313.
- Spiegelhalter, D. J., N. G. Best, B. P. Carlin, and A. V. d. Linde. 2002. Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society B* **64**:583-639.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, England.
- Studds, C. E. and P. P. Marra. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. *Ecology* **86**:2380-2385.
- Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: a package for running WinBUGS from R. *Journal of Statistical Software* **12**:1-16.

- Team, R. D. C. 2009. R: A language and environment for statistical computing. R Foundation for statistical computing, Vienna, Austria.
- Wassenaar, L. and K. Hobson. 2003. Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. *Isotopes in Environmental and Health Studies* **39**:211-217.
- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution* **17**:76-83.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *The American Naturalist* **100**:687-690.
- Wingfield, J. C. 1984. Influence of weather on reproduction. *Journal of Experimental Zoology* **232**:589-594.
- Woodbridge, B., K. K. Finley, and S. T. Seager. 1995. An investigation of the Swainson's hawk in Argentina. *Journal of Raptor Research* **29**:202-204.

Table 1. Correlation of the measures of feather condition as well as the residuals of body condition standard major axis (SMA) regression of Swainson's Hawks nesting in Butte Valley, California, USA and trapped on their wintering grounds in La Pampa, Argentina. Above the diagonal are relationships among the variables from feathers that were freshly molting. Below the diagonal are from feathers grown in the season they were trapped based on stable isotope results (see text for more details).

| | ADG ¹ | Condition ² | CORT ³ | FB ⁴ |
|-----------|------------------|------------------------|-------------------|-----------------|
| ADG | 1 | 0.61* | 0.16 | 0.00 |
| Condition | -0.03 | 1 | 0.40 | 0.17 |
| CORT | 0.05 | -0.04 | 1 | -0.38 |
| FB | 0.08 | 0.21 | -0.36 | 1 |

¹ ADG, Average Daily Growth of the feather based on standard ptilochronology measures (Grubb 1989)

² Condition, Residuals of standard major axis regression of wing chord and weight. Separate regressions were performed for males and females.

³ CORT, concentration of corticosterone (pg/mL) in the 50mm tip of the feather.

⁴ Number of fault bars observed in the remiges and retrices in feathers with little or no wear when the individual was trapped.

* indicates $P < 0.05$

Table 2. Calculated values from a daily nest survival analysis using Bayesian hierarchical models calculated from a reversible jump Markov Chain Monte Carlo for Swainson's Hawks nesting in Butte Valley, California, USA from 2008-2010. Marginal probability reflects the amount of time a chain spent with a particular variable. Location (i.e. Argentina versus CA) was determined through stable isotope analysis.

| | | Marginal Probability | Mean | SD | 2.50% | Median | 97.50% |
|--------|--------------------------------|-------------------------|--------|------|-------|--------|--------|
| Male | Argentina DGB ¹ | 0.96 | 4.3 | 2.3 | 0 | 4.1 | 9.0 |
| | CA DGB | 0.81 | -1.2 | 0.8 | -2.7 | -1.3 | 0 |
| | Old FB ² | 0.91 | -3.4 | 2.0 | -7.3 | -3.6 | 0 |
| | New FB | 0.11 | 0.0 | 0.2 | -0.2 | 0 | 0.4 |
| | Argentina CORT ³ | | | | | | |
| | CA CORT | 0.76 | 1.1 | 0.9 | 0 | 1.2 | 3.0 |
| | Condition ⁴ | 0.07 | -00.05 | 0.22 | -0.9 | 0 | 0 |
| Female | Argentina | 0.02 | 0 | 0 | 0 | 0 | 0 |

| DGB | | | | | | |
|-----------|------|------|------|------|---|------|
| CA DGB | 0.15 | -0.1 | 0.3 | -1.0 | 0 | 0.2 |
| Old FB | 0.33 | 0.2 | 0.7 | -0.5 | 0 | 2.2 |
| New FB | 0.28 | -0.2 | 0.8 | -2.5 | 0 | 1.2 |
| Argentina | | | | | | |
| CORT | 0.02 | 0 | 0 | 0 | 0 | 0 |
| CA CORT | 0.02 | 0 | 0 | 0 | 0 | 0 |
| Condition | 0.06 | 0.01 | 0.10 | 0 | 0 | 0.30 |

¹ ADG, Average Daily Growth of the feather based on standard ptilochronology measures (Grubb 1989)

² FB, Number of fault bars observed in the remiges and retrices in feathers with little or no wear when the individual was trapped (new) or noticeable wear and fading on the feather (old).

³ CORT, Concentration of corticosterone (pg/mL) in the 50mm tip of the feather.

⁴Condition, Residuals of standard major axis regression of wing chord and weight.

Separate regressions were performed for males and females.

Table 3. AIC_c table for results of number of fledglings produced against measures of feather condition from Swainson's Hawks nesting in Butte Valley, California, USA from 2008-2010. Location (i.e. Arg versus CA) was determined through stable isotope analysis.

| | Model | ΔAIC_c | Deviance | Weight |
|--------|----------------------|----------------|----------|--------|
| | Null | 0.7 | 10.5 | 0.18 |
| | CA CORT ¹ | 2.7 | 10.5 | 0.07 |
| | Arg CORT | 1.9 | 9.7 | 0.10 |
| Male | CA ADG ² | 1.8 | 9.6 | 0.10 |
| | Arg ADG | 0 | 9.8 | 0.26 |
| | New FB ³ | 2.6 | 10.5 | 0.07 |
| | Old FB | 0.3 | 10.5 | 0.22 |
| | Null | 0.1 | 12.1 | 0.14 |
| | CA CORT | 0.4 | 12.4 | 0.12 |
| Female | Arg CORT | 0 | 12 | 0.15 |
| | CA ADG | 0.1 | 12.1 | 0.14 |
| | Arg ADG | 0.1 | 12.1 | 0.14 |

| | | | |
|--------|-----|------|------|
| New FB | 0 | 12 | 0.15 |
| Old FB | 0.1 | 12.1 | 0.14 |

¹ ADG, Average Daily Growth of the feather based on standard ptilochronology measures (Grubb 1989)

² FB, Number of fault bars observed in the remiges and retrices in feathers with little or no wear when the individual was trapped (new) or noticeable wear and fading on the feather (old).

³ CORT, Concentration of corticosterone (pg/mL) in the 50mm tip of the feather.

Table 4. AIC_c table for results of incubation onset against measures of feather condition from Swainson's Hawks nesting in Butte Valley, California, USA from 2008-2010.

Location (i.e. Arg versus CA) was determined through stable isotope analysis.

| | Model | ΔAIC_c | dev | Weight |
|--------|------------------------|----------------|------|--------|
| Male | Null | 0.6 | 10.5 | 0.16 |
| | Arg ADG ¹ | 0 | 9.9 | 0.22 |
| | CA ADG | 1.8 | 10.5 | 0.09 |
| | Arg CORT ² | 0.6 | 10.5 | 0.16 |
| | CA CORT | 2.6 | 10.5 | 0.06 |
| | Old FB ³ | 0.3 | 8.2 | 0.19 |
| | New FB | 2.6 | 10.5 | 0.06 |
| | Condition ⁴ | 2.6 | 10.5 | 0.06 |
| Female | Null | 0 | 12.1 | 0.27 |
| | Arg ADG | 2 | 12.1 | 0.10 |
| | CA ADG | 1.9 | 12.1 | 0.10 |
| | Arg CORT | 2 | 12.1 | 0.10 |

| | | | |
|-----------|-----|------|----------|
| CA CORT | 1.6 | 11.7 | 0.121009 |
| Old FB | 2 | 12.1 | 0.099074 |
| New FB | 1.9 | 12 | 0.104153 |
| Condition | 1.9 | 12 | 0.104153 |

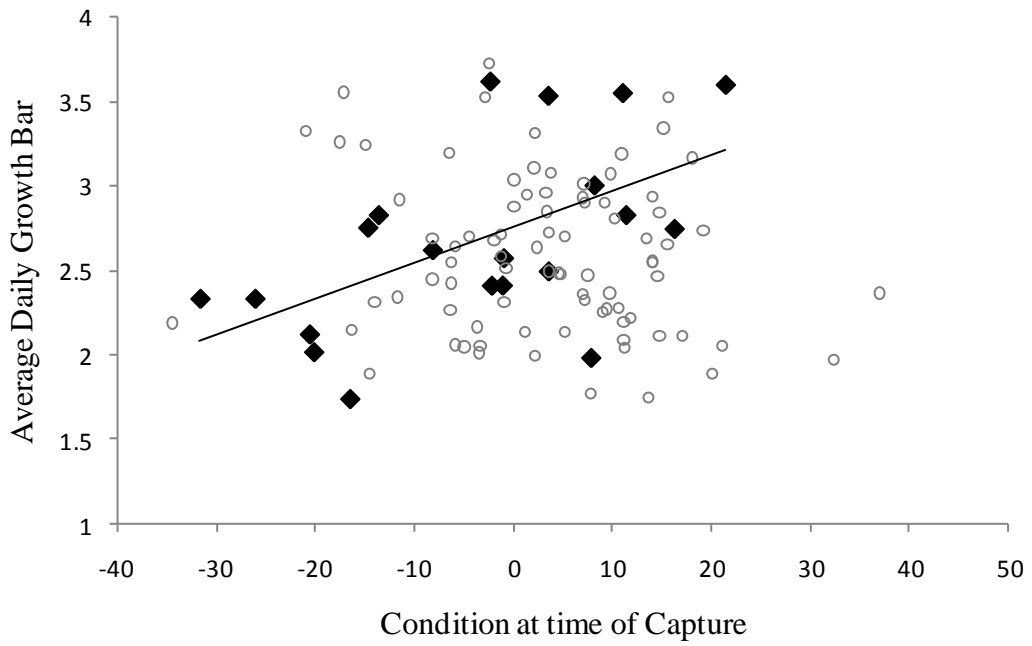
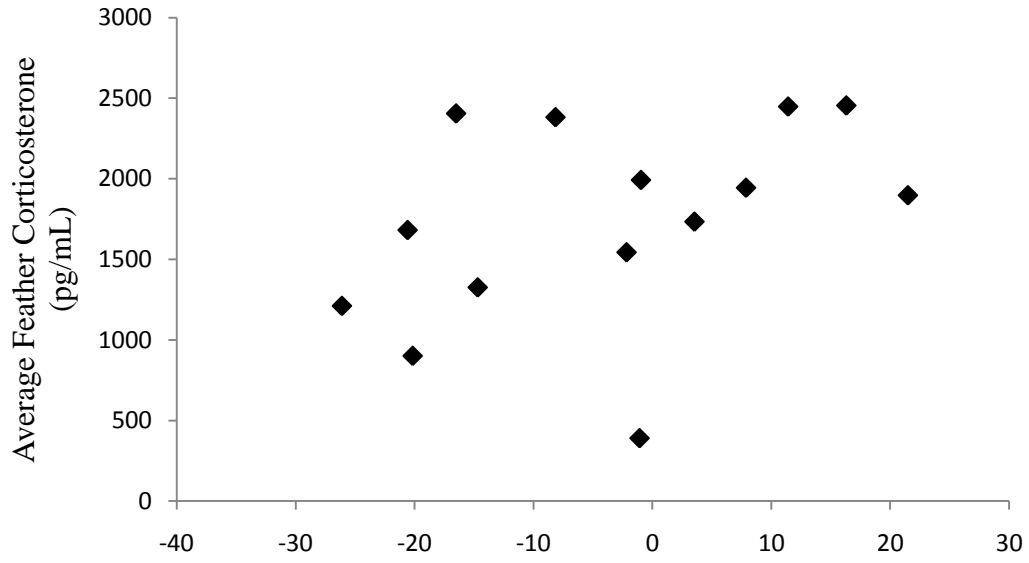
¹ADG, Average Daily Growth of the feather based on standard ptilochronology measures (Grubb 1989)

²CORT, Concentration of corticosterone (pg/mL) in the 50mm tip of the feather.

³FB, Number of fault bars observed in the remiges and retrices in feathers with little or no wear when the individual was trapped (new) or noticeable wear and fading on the feather (old).

⁴Condition, Residuals of standard major axis regression of wing chord and weight. Separate regressions were performed for males and females.

Figure 1. (A) Relationship between corticosterone (CORT) concentration in the last 50mm of a newly grown secondary covert and body condition based on a standard major axis (SMA) regression where condition for male and female Swainson's hawk was calculated separately. (B) Relationship between average daily growth of freshly grown feathers (open circles), feathers still in sheath and therefore growing at the time of capture (closed diamonds) and body condition based on the SMA regression. Individuals were captured from 2008-2010 in Butte Valley, California, USA and 2010 in La Pampa, Argentina.



Chapter 6 - Summary, Conclusions and Recommendations

The population dynamics of Swainson's Hawks are complex and a long-term dataset can provide researchers with substantial insight into a number of aspects of its ecology. The relative ease of study and longevity of this study has, in many cases, provided us insight that we could not otherwise obtain.

Plumage polymorphisms are common among *buteo* species in North America, but little is known about them (but see Schmutz and Schmutz 1981, Arcese and Fitzner 1982). This study has contributed to that small pool of knowledge, and provides some tantalizing evidence of mechanisms that allow this variation to persist across the landscape. While dark morph individuals in our population have slightly higher adult survival, it did not appear to translate into fitness benefits, at least with the precision we could measure (i.e., recruitment rates and lifetime reproductive success). Thus, we currently do not detect a selective advantage for any morph. While it could be that fitness differences are too subtle for us to detect, it is also possible that the high prey abundances in the study area that lead to this study's inception could mask differences by providing adequate prey to individuals of all morph types.

We provide evidence that sexual selection is occurring in Swainson's Hawks. Specifically, males select for females with a similar phenotype as their mother. In contrast, females have no mate preference based on parental phenotype. While evolutionary theory predicts that males of species that invest heavily in offspring should be choosy (e.g., Trivers 1972), it remains unclear what ultimate mechanism, if any, were responsible for the development of male mate choice. It is unreasonable to suspect that females do not select mates based on a criterion, but rather likely choose mates based on

other factors (e.g., territory quality). Other explanations, such as ectoparasite load and thermal ecology should be investigated to determine potential benefits that could translate into fitness benefits. If, as the survival data suggests, dark individuals have higher survival, the preponderance of dark and intermediate individuals may instead result from an introgression of light alleles from the Great Plains, where most individuals are light morphs (Wheeler 2003). Such a genotype-by-environment interaction has often been hypothesized to allow for polymorphisms to exist between populations, the selective pressures of different environments allowing different morphs to thrive in different areas (Galeotti and Rubolini 2004). The subsequent mixing of populations creates greater variation than we would expect based on the selective pressures present in the environment being investigated. However, it remains unclear why introgression of alleles would be so one-sided (i.e. why there isn't a greater number of intermediate and dark individuals throughout the Great Plains). Selection could be stronger for light individuals in the Great Plains than dark individuals in the Great Basin. Alternatively, the Great Plains population could be much larger, effectively swamping any variation that enters the Great Plains population. However, the fact that there is no genetic population structure between the Great Plains and Great Basin populations suggests that there must indeed be significant gene flow and selection acts against dark alleles in the eastern end of their range.

Future investigations should examine the possibility that there is segregation on the wintering grounds in addition to potential benefits on the breeding grounds. Additionally, the genetic underpinnings of this polymorphism need to be investigated, as the melano-cortin-1-receptor gene that is responsible for similar plumage

polymorphisms in a number of species does not seem to play a significant role in the polymorphism observed in *buteos* (Hull et al. 2010). Additionally, studies should be taken up examining polymorphisms in other *buteo* species, as several exhibit similar east-west clines in melanization (Wheeler 2003). Given the apparent convergence of morphs in several species, it is reasonable to hypothesize that a common mechanism may create the clines observed across these species and those potential mechanisms should be investigated further.

Our data on carry-over effects suggest that the level of stress and an individual's condition in Argentina do not influence breeding timing or reproduction in our population. While our measure of condition represented only a snapshot of that individual at some unknown point during the wintering season, it indicates that individuals can recover from poor condition on their wintering grounds to breed successfully in our population. Again, the high prey densities (Woodbridge 1991, Whisson et al. 1999) may assist individuals in rapidly acquiring resources to overcome such poor condition. However, it is reasonable to hypothesize that individuals that perform poorly in Argentina would delay migration, arrive on the breeding grounds later, and begin breeding later. While we could not assess potential correlations between arrival date and beginning of breeding, observational data suggest that there is a correlation between these two in this population (C.W.B. pers. obs.). However, this assumption should be more rigorously tested in the future.

While stress on the wintering grounds did not influence reproduction in our population, individuals that successfully fledged offspring were more likely to be stressed. These data do not support current life-history theory, which hypothesizes that

long-lived species should minimize stress from reproduction in favor of future reproduction, which should maximize fitness. These data suggest that there may be a cost to reproduction, even in areas with high prey availability and future work should focus on carry-over effects of previous reproduction to determine if that plays a role in future reproduction.

Long-term studies, such as this one, provide great insight and opportunity for research into ecological and evolutionary questions, as well as conservation issues that could not be addressed without a temporal scale. This study, like all observational studies, has flaws. We cannot directly assess fitness due to myriad factors (e.g., emigration, incomplete detection probabilities); however, we can produce reasonable indices of fitness (e.g., lifetime reproductive success, recruitment rates of offspring). Thus, future studies could benefit from a more experimental approach. For example, performing nestling swaps among paired nests to examine the Oedipal complex that these birds may have could provide significant power and insight into our observation of sexual selection. Despite these limitations, we were able to gain insight into the ecology and evolution of Swainson's Hawks in and around Butte Valley, California.

Literature Cited

Arcese, P. and R. E. Fitzner. 1982. Plumage polymorphism in Swainson's Hawk (*Buteo swainsoni*): testing a hypothesis of apostatic selection of predators. Pacific Northwest Labs., Richland, WA (USA).

- Galeotti, P. and D. Rubolini. 2004. The niche variation hypothesis and the evolution of colour polymorphism in birds: a comparative study of owls, nightjars and raptors. *Biological Journal of the Linnean Society* **82**:237-248.
- Hull, J. M., D. P. Mindell, S. L. Talbot, E. H. Kay, H. E. Hoekstra, and H. B. Ernest. 2010. Population structure and plumage polymorphism: The intraspecific evolutionary relationships of a polymorphic raptor, *Buteo jamaicensis harlani*. *BMC Evolutionary Biology* **10**:224.
- Schmutz, S. M. and J. K. Schmutz. 1981. Inheritance of color phases of ferruginous hawks. *Condor* **83**:187-189.
- Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136-179 in B. Campbell, editor. *Sexual Selection and the Descent of Man, 1871-1971*. Aldine, Chicago.
- Wheeler, B. K. 2003. *Raptors of Western North America: The Wheeler Guides*. Princeton University Press, Princeton, NJ.
- Whisson, D. A., S. B. Orloff, and D. L. Lancaster. 1999. Alfalfa yield loss from Belding's ground squirrels in northeastern California. *Wildlife Society Bulletin* **27**:178-183.
- Woodbridge, B. 1991. Habitat selection by nesting Swainson's hawk: a hierarchical approach. Thesis. Oregon State University, Corvallis, OR.