FACTORS INFLUENCING VIGILANCE WHILE FEEDING IN REINTRODUCED

CALIFORNIA CONDORS (*GYMNOGYPS CALIFORNIANUS*)

By

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ABSTRACT

FACTORS INFLUENCING VIGILANCE WHILE FEEDING IN REINTRODUCED
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Pressure from potential predators makes vigilance critical for an individual's
survival, especially during times of vulnerability. California condors (*Gymnogyps
californianus*), with their heavy bodies and large, broad wings, are slow to take-off. This
makes vigilance an essential survival behavior for condors due to their susceptibility
when feeding on carcasses. Relatively high overall mortality among reintroduced
condors has raised questions regarding the suitability of release candidates. Reduction in
this overall mortality is of primary concern to the California Condor Recovery Program.
I investigated factors influencing vigilance in 31 reintroduced California condors while
feeding on proffered carcasses at a primary release site in Southern California. I
measured individual vigilance, via scanning frequency, and a suite of factors previously
shown to influence vigilance. I used an information theoretic approach to determine
which of a set of explanatory models best fit the variation in anti-predator scanning
frequency observed in my data. The best fitting model incorporated the following
variables in order of decreasing importance: a negative correlation with the number of
individuals at the carcass feeding site, a negative correlation with Julian date, a positive
correlation with focal bird age, sex (males were more vigilant than females), and a
negative correlation with ambient temperature. Examination of survival behaviors such

as vigilance may allow for more rapid identification of problematic behaviors in release

candidates, as well as providing insight for aviculturists and field managers regarding

foci for future management efforts.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF APPENDICES

INTRODUCTION

For most species, individual survival is contingent upon exhibition of proper mortality avoidance behaviors. Conspecific and antipredator vigilance while foraging is an important aspect of mortality avoidance and a popular topic of behavioral research (Elgar 1989, Quenette 1990). Much of this research has focused on both environmental factors and individual behavioral mechanisms contributing to individual and group vigilance at times of vulnerability, such as when feeding (Lazarus and Symonds 1992, Poysa 1994, Burger et al. 2000, Burger 2001).

Many environmental factors have been shown to contribute to an individual's exhibited level of vigilance (Elgar 1989, Quenette 1990). Distance to cover (Lazarus and Symonds 1992, Poysa 1994, Burger et al. 2000), presence of visual obstructions (Metcalfe 1984, Burger 2001, Whittingham et al. 2004), group size (Pulliam and Caraco 1984, Roberts 1996, Bednekoff and Lima 1998, Beauchamp and Ruxton 2003), spatial position within the group (Burger et al. 2000, Beauchamp 2001, 2003, Arenz 2003, Di Blanco and Hirsh 2006, Dias 2006, Fernández-Juricic and Beauchamp 2008), presence of conspecific kleptoparasites (Knight and Knight 1986, Goss-Custard et al. 1999, Beauchamp 2001), and temperature (Beveridge and Deag 1987, Pravosudov and Grubb 1995) have all been shown to significantly affect vigilance behavior in foraging groups.

An individual's unique attributes may also contribute to exhibited vigilance levels. Several studies have found an inverse relationship between vigilance and social rank (Rasa 1989, Yaber and Herrera 1994, Pravosudov and Grubb 1999). Age

1

(Beveridge and Deag 1987, Rasa 1989, Alberts 1994, Arenz and Leger 1997) and sex

(Beveridge and Deag 1987, Alberts 1994) have also been shown to affect vigilance level.

The social environment within which individuals are raised, especially with regard to

parents and adult conspecifics, can also have a significant impact on the development of

vigilance behavior (Dowell 1988, 1989, Marshall and Black 1992). This may be

especially relevant to managers working in reintroduction programs where captive-

rearing restricts parent-offspring interactions and so restricts learning opportunities for

progeny. It is generally accepted that social and foraging skills learned from parents

impart essential knowledge needed for survival, and individuals reared without parents

may be at a disadvantage after release into the wild (Black and Owen 1989, Raveling et

al. 2000, Black et al. 2007). Concerns regarding these limitations and research indicating

that training in captivity can have long term effects on post release behavior (Azevedo

and Young 2006) have led aviculturists with the California Condor Recovery Program to

"train" nestling and juvenile condors with unique methods, such as use of adult-like

puppets, power-pole aversion training, and use of actual adult condor mentors prior to

release (Appendices A, B).

　　　　During times of vulnerability, such as when an individual cannot adequately sense

their surroundings (Burger 2001) or when they are in a position that makes them

susceptible to potential aggressors (Lima and Bednekoff 1999), vigilance is especially

important. Large soaring birds, such as vultures and condors, have long wings which

make take off from the ground difficult; often a run, to gain speed, is necessary to take

flight (Koford 1953, Mundy et al. 1992).

Carcasses often attract large, aggressive predators making them a potentially dangerous place to feed. Known condor predators, that frequent carcasses, include golden eagles (*Aquila chrysaetos*), mountain lions (*Puma concolor*), and coyotes (*Canis latrans*). In addition to these, bobcats (*Lynx rufus*), wild pigs (*Sus scrofa*), feral dogs (*Canis familiarus*), and black bears (*Ursus americanus*) have all been observed feeding on proffered carcasses within reintroduced condor ranges (C. West, personal observation). Vigilance at carcasses is essential for condors due to their aforementioned vulnerability when on the ground. This point is supported by condors observed preference for carcasses on open slopes or near cliffs (Koford 1953) which afford them clear views of their surroundings. Feeding sites with such attributes may allow early detection of potential predators providing the opportunity for a condor to plan and execute a safe escape. Additionally, such sites may allow a condor to identify nearby or newly arriving conspecifics and adjust their behavior according to dominance differences.

I examined the influence of sociality and abiotic factors on California condors (*Gymnogyps californianus*) feeding at proffered carcasses. To accomplish this, I evaluated alternative hypotheses, expressed as models, in an information theoretic approach. Examination of survival behaviors, such as vigilance, expands our knowledge of this species, may allow for more rapid identification of problematic behavior in release candidates, and may provide invaluable information for managers and breeding programs regarding appropriate foci for future rearing and management efforts.

METHODS

<u>Field Observations</u>

Condor field observations were made at Hopper Mountain Wildlife Refuge, Hopper Mountain, Ventura County, California from July to August of 2003 and June to August of 2004. Tracking and identification of free-flying condors was achieved via two patagial-mounted tracking and identification packages placed by United States Fish and Wildlife Service (USFWS) biologists prior to release or fledge from wild nests. Each bird carried two color-coded, numbered, vinyl, wing-tags, for visual identification, and either two radio transmitters for direct radio tracking or one radio transmitter and one satellite uplink, global positioning system transmitter for remote sensing purposes. Two to three stillborn, dairy-calf carcasses, were placed every two to three days at an established feeding site (small hill protected by an electrified perimeter fence). To reduce the potential for condor observation of carcass placement activities, and as a result associating humans with food, all carcasses were placed at night.

To assess the effect of ease of take off on vigilance, atmospheric measurements which may contribute to lift and measurements regarding the physical environment around carcasses were recorded. Specific placement of carcasses varied within the feeding site, so measurements of the physical environment were collected at the time of placement for each carcass. Slope aspect was documented using visual approximation and a compass bearing. Five slope angle measurements were taken using a clinometer at slope aspect, plus and minus 30 degrees from slope aspect, and plus and minus 60

4

degrees from slope aspect. Angle measurements on each carcass were averaged to give a measure of average down-slope angle that could give a bird advantage in a running take-off. To assess the effect of proximity of potential predator cover on vigilance, distance was measured from each carcass to the nearest item of sufficient height to provide cover to approaching ground-based predators, such as coyote, mountain lions, black bear, or bobcats.

Feeding activity was recorded with a digital video camera from the initiation of feeding until feeding ended, or up to four hours (hrs) of footage. Feedings were filmed from either a camouflage pop-up blind or permanent camouflaged observation blind, approximately 50 meters (m) from the carcass placements, using a Canon ZR70 MC mini digital video camcorder (Canon Incorporated, Tokyo 146-8501, Japan) with a 1.9x tele-converter and a polarizing filter to reduce glare. Feeding sessions were filmed based on number of birds present at the carcass and amount of time filming had been ongoing with no change in make-up of that specific group.

All condors visiting the feeding site were identified via patagial tags and arrival and departure times for each individual bird were recorded. Wind speed was measured with a Hanson Hand-held Anemometer (Thunderhead Technologies, Taunton, MA, USA) mounted one m above the ground and placed outside the perimeter fence, approximately 15 m from carcass placements. The white anemometer was covered with desert camouflage tape on non-moving parts and brown permanent ink on the rotational parts to prevent disturbance to feeding condors. Wind measurements were recorded every 10 minutes (mins) as m per 10 mins and later converted to m per second (s) for analyses.

Wind direction was determined every 10 mins from observation of strings hanging from

the perimeter fence nearest to the carcasses (approximately 10 m) and estimated using

compass bearing. Temperature and relative humidity were recorded every five mins,

using an Onset HOBO RH/Temp Pro-H08 data-logger housed in an Onset RS1 Solar

Radiation Shield (Onset Computer Corporation, Pocasset, MA, USA). The data-logger

was mounted one m above ground, alongside the anemometer, and covered with

camouflaged burlap material to prevent disturbance to the feeding condors. Atmospheric

pressure data was collected after completion of field work from records available through

The Weather Underground (http://www.wunderground.com/, The Weather Underground

Inc.). These data were collected at the Upper Ojai weather station (ID: KCAOJAI1) in

Ojai, California, 26 km from the field site. Atmospheric pressure, temperature, and

humidity data were used to generate a measure of air density, which affects lift on the

wing of a bird taking-off. Records of last feeding event, prior to each observation day,

for each condor, were obtained from personal notes and records at the Hopper Mountain

Refuge Complex office in Ventura, California and the Ventana Wildlife Society field

office in Big Sur, California.

Zoo Data Collection

Background information on rearing methodologies from hatch to 180 days of age

(estimated average fledge age) was collected for each individual observed in the field

from records at rearing and release facilities. Information related to hatch date, genetic

parents, rearing method (puppet/parent), and transfer dates to field locations was obtained

from the California condor studbook (Mace 2004). The number of days each puppet-reared bird was exposed to hand puppets and information related to the identity, age, and length of exposure to all pen-mates/mentors and all birds observable through mentor observation windows was obtained for all birds directly from individual condor files at the Los Angeles Zoo, Los Angeles, California; the San Diego Wild Animal Park, Escondido, California; and the Ventana Wilderness Society Big Sur field office, Big Sur, California.

Footage Organization and Sampling

All video footage was reviewed and all start and stop times for feeding bouts were recorded for each individual. Feeding bouts initiated when the bill of a non-feeding individual made contact with a carcass. Feeding bouts ended when individuals stopped feeding for longer than 20 s, moved a bird length or more from the feeding group for longer than 20 s, were obscured by other birds such that behavior could not be determined, or they exited the camera frame for long enough that behavior could not be determined. Occasionally, the hierarchy structure within the flock broke down and all individuals fed aggressively at once in a scramble competition manner which has been shown to affect vigilance in other species (Beauchamp and Ruxton 2003). This manner of feeding was much less typical than controlled feedings. In controlled feedings, fewer than 10 individuals fed at any one time, a single most dominant individual controlled the carcass, and non-feeding birds often waited at the periphery of the feeding area for

feeding opportunities. I chose to focus on the more typical social situation and so did not record feeding bout information for scramble competition periods.

To determine an adequate sample period length, several sample durations were initially tested to assess variation in scanning behavior. The standard deviation of scan duration per s stabilized around 150 s, however, a 180 s sample interval was chosen to be conservative while still retaining a sample size likely to retain adequate statistical power. Bouts meeting the 180 s minimum length requirement, with a minimum of 24 hrs separating sequential bouts per individual to maximize independence, were tallied. Bouts for sampling were randomly selected from those available for each individual, with a minimum of ten required for inclusion and a maximum of 15 used per individual. Initially, I intended to use averaging across samples for each individual in order to eliminate individual variation and achieve more statistical independence. However, mixed effects modeling analyses revealed that individual variation was similar in structure to the variation of the entire dataset. Since data dependency was not an issue, I was able to use all samples from all individuals and treat each as an independent data point.

Feeding bouts were sampled using a Psion Walkabout programmable data logger (Psion Teklogix Inc., Mississuaga, Canada) using the Noldus Observer 5.0 software package (Noldus Information Technology, Wageningen, Netherlands) to capture scanning duration and frequency, aggressive interactions between birds, and other non-scanning behavior durations. Outside versus within feeding group scanning was determined by head motion and orientation. Sampling included real-time documentation

of each individual bout of each of the following behaviors: time spent scanning the area outside the feeding group, time spent scanning the area within the feeding group, receipt or initiation of conspecific aggression, feeding, walking, and other. As my focus was on anti-predator behavior, only bouts of time spent scanning the area outside the feeding group were used for analyses to avoid interpretation difficulties that may result from including within group scans (Beauchamp 2001). For sampling purposes, feeding bouts were sampled from the initiation of feeding by the individual that was the primary focus of that sampling period (focal individual, as defined by Martin and Bateson 1993) and terminated when the 180 s sampling period ended.

Analysis

Due to a lack of previous research pertaining to new world vultures and vigilance, an *a posteriori* model selection and inference strategy was implemented to investigate influential variables and select competitive models (Stauffer 2008). Such methods typically produce 'exploratory' models that are not necessarily considered 'predictive' (Burnham and Anderson 2002); however, I believe that information obtained from such analyses can have significant scientific and management implications.

Dependent variables used for direct measure of vigilance behavior were: scanning time, scanning frequency, and mean scan duration. Scanning time was recorded as total time (s within the 180 s sample period), spent scanning areas outside of the feeding group. Scanning frequency was recorded as number of scans per sample. Mean scan duration was measured as mean duration of individual scan bouts within a sample period,

excluding bouts cut short by termination of the sample at the 180 s cut-off. Preliminary data screening indicated that variation in mean scan duration was small, and as a result all variation in scanning was related directly to scan frequency. All subsequent analyses were performed on scan frequency as the sole vigilance measure.

Independent variables were initially grouped into four categories; individual characteristics, pre-fledge age socialization strategy, feeding group social factors, and environmental factors; to simplify preliminary use in multiple regression based variable selection routines. Individual characteristics included: focal individual sex, focal individual age (in months, with a maximum of 120 for individuals this age and older, indicating fully mature and experienced adults), time in the wild (in months), time since focal individual last fed (in days), and puppet or parent rearing type. Pre-fledge age (180 days) socialization strategy included: total number of social partners, total number of adult social partners, total number of adult male social partners, total number of adult female social partners, socialized or not with juveniles, socialized or not with same age conspecifics, total social time, total social time with adults, total social time with juveniles, and total social time with same age conspecifics. Feeding group social factors included: male to female sex ratio, average group age, age of oldest bird, difference between focal bird age and average age of the rest of the group, number of birds at the site, continuous time since feeding initiated at that feeding site, rate of aggressive behavior received by the focal bird from conspecifics, and time per observation that the focal bird received aggressive behavior from conspecifics. Environmental factors included: slope angle, distance to nearest potential predator cover, Julian date, time of

day, wind speed, wind direction, atmospheric pressure, temperature, relative humidity, and air density.

Stepwise variable selection routines as well as standard multiple regression analyses were employed on each group utilizing all samples and using NCSS/PASS statistical software (Hintze 2001). After the most influential independent variables within each group were identified, all variables were combined into a single data set for further analysis. An "all-possible variable selection routine" was used, again employing the NCSS/PASS statistical package, to generate three competitive models for each covariate range (e.g. model with one variable, two variables, and so on, including the global model). All models were analyzed using least squares, multiple regression to generate Akaike Information Criterion (AIC) values with statistical freeware Program R (R Development Core Team 2007). Values were then adjusted for small-sample bias (AIC_c) (Hurvich and Tsai 1989). The resulting AIC_c values were used to examine the difference between the best fitting model and competing models (ΔAIC_c) and generate AIC weights (W_{AICc}) for use in model ranking (Burnham and Anderson 2002), with the best fitting model having the greatest W_{AICc}. Due to very small differences in resulting AIC_c values, model averaging was used to clarify the contribution of all variables required to account for 95% of the variation within the dataset and generate new coefficients for the resulting averaged model (Burnham and Anderson 2002). All data was used with focal birds individually sampled 10 to 15 times; pseudoreplication was addressed by employing a mixed-effects modeling approach using bird zoo studbook number as a grouping variable (Stauffer 2008). The generated random effects did not significantly improve top models.

This result indicates that all samples were statistically independent, the above detailed analysis was appropriate, and subsequent results should be considered robust (n = 418). A final multiple regression was run to further investigate the variation in mean scan bout duration related to the top chosen model.

An *a posteriori* fit test was performed on both the top ranked model and the model generated by the model averaging procedure. My initial dataset was randomly split into 75% and 25% groupings to create prediction and test data sets respectively. Prediction intervals were generated with Minitab 15 (Minitab Inc. 2006) and the proportion of the test set that fell within these intervals was estimated.

RESULTS

I sampled 418 feeding bouts from 31 individual reintroduced condors. Data screening revealed a strong correlation between total scan duration and scan frequency (Spearman correlation coefficient = 0.81). Initial analyses of factors influencing scan rate using stepwise regression routines suggested inclusion of four primary variables for further analyses. These included: numbers of condors at feeding site, Julian date, focal bird age, and focal bird sex. Variation in mean square error and the amount of variation in the dependent variable accounted for by various combinations of independent variables was examined during multiple regression variable omission routines (NCSS). These analyses indicated additional variables that should also be retained for examination in "all possible regression" model building procedures. These included: total number of condors socialized to focal bird prior to fledge age, temperature, and number of aggressive interactions received by the focal bird during the sample period. Using the "all possible regression" routine in NCSS and these seven remaining variables, 20 models were selected for further use in the information theoretic analysis.

The best model, having the highest W_{AICc}, included the following dependent variables (presented in order of importance according to summed corrected W_{AICc} (Table 1)): the number of birds at the feeding site (negatively correlated with scan frequency), Julian date (negatively correlated with scan frequency), focal bird age (positively correlated with scan frequency), focal bird sex (males were more vigilant than females),

Table 1. Relative importance and contribution of individual independent variables in explaining the variation in anti-predator vigilance scan rate while feeding by California condors at Hopper Mountain Wildlife Refuge, Ventura County, California, June through August 2003 and 2004.

Variables	Summed corrected W_{AICc}
Number condors at feeding site	1.00000
Julian Date	0.99996
Focal bird age at sample (in months)	0.99989
Focal bird sex	0.95188
Temperature	0.69513
Aggressive interactions received	0.48456
Number pre-fledge socials	0.46422

Numbers are W_{AICc} (see text for calculation details) summed over all candidate models containing the variable in question.

and ambient temperature at the time of the sample (negatively correlated with scan frequency) (Tables 2, 3). All individual variables included in this model significantly affected scan rate (Table 3). While this model did rank highest according to AIC_c value, the 2nd, 3rd (global model), and 4th ranked models were all within 0.23 AIC_c units of the top ranked model (Table 2). Due to the relative similarity in amount of variation accounted for amongst highly ranking models, model averaging was used, inclusive of the top eight models, to account for 95% of the variation within the dataset. Multiple regression analysis of the top model against mean scan bout duration revealed a lack of variation within this dependent variable (Adjusted $R^2 = 0.0042$).

Goodness of fit tests showed high levels of predictability for vigilance scan rate with both the top and averaged models, 94% and 91% respectively. Fit testing was performed on the same dataset that was used to generate the models in question, so predictability values should be viewed cautiously. While these fit tests do appear to show good fit for both of these models and high predictability, generated prediction intervals were quite broad. A test set of randomly generated numbers within the range of my actual dependent variable test set, exclusive of one potential outlier value to be more conservative, predicted vigilance scan rates for my top and averaged models with 79% and 71% accuracy respectively.

Table 2. Top eight ranked and null models which together explained 95% of variation in anti-predator vigilance scan rate while feeding by California condors at Hopper Mountain Wildlife Refuge, Ventura County, California, June through August 2003 and 2004.

Model Identifier	Model	K	AIC_c	ΔAIC_c	W_{AICc}	Rank	R^2
Model 1	A+B+C+D+E	7	2308.29	0.000	0.1783	1	0.324
Model 2	A+B+C+D+E+F	8	2308.45	0.153	0.1652	2	0.326
Global Model	A+B+C+D+E+F+G	9	2308.46	0.169	0.1638	3	0.328
Model 4	A+B+C+D+E+G	8	2308.52	0.226	0.1593	4	0.326
Model 5	A+B+C+D+F	7	2309.86	1.570	0.0813	5	0.322
Model 6	A+B+C+D+F+G	8	2310.05	1.753	0.0742	6	0.323
Model 7	A+B+C+D	6	2310.12	1.826	0.0715	7	0.320
Model 8	A+B+C+D+G	7	2310.53	2.238	0.0582	8	0.321
Null Model	(Intercept)	1	2467.00	158.712	6E-36	20	N/A

A = Number of condors at feeding site, B = Julian date, C = Focal bird age, D = Focal bird sex, E = Temperature, F = Number of aggressive interactions received from conspecifics by focal bird, G = Total number of condors socialized to focal bird pre-fledge.

K = Total number of estimated regression parameters (independent variables) including the intercept and σ^2 (measure of variance).

Table 3. Estimated coefficients and standard error for top ranked and averaged models of anti-predator vigilance scan rate while feeding by California condors at Hopper Mountain Wildlife Refuge, Ventura County, California, June through August 2003 and 2004.

Variables	Coefficient and error in Top Ranked Model	Averaged Model
(Intercept)	24.45 ± 2.38 *	23.496 ± 2.367 ◆
Number Birds at Feeding Site	-0.332 ± 0.027 *	-0.335 ± 0.028 ◆
Julian Date	-0.045 ± 0.011 *	-0.047 ± 0.011 ◆
Focal Bird Age	0.025 ± 0.006 *	0.026 ± 0.007 ◆
Focal Bird Sex	-0.887 ± 0.372 *	-0.932 ± 0.374 ◆
Temperature	-0.104 ± 0.053 *	-0.072 ± 0.037
Aggressive Interactions received	N/A	0.079 ± 0.054 ☠
Number pre-fledge socials	N/A	0.043 ± 0.031 ☠

* 95% confidence interval did not include zero

◆ 95% confidence interval did not include zero in any included models

☠ 95% confidence interval included zero in all included models

Sign of coefficient indicates whether there is a positive or negative correlation with the dependent variable (for sex, males were designated 0 and females 1, males were more vigilant than females).

DISCUSSION

<u>Top Model</u>

The most important factors influencing vigilance in reintroduced California

condors included in this study were: the number of condors present at the feeding site

(negatively correlated with scan frequency), Julian date (negatively correlated with scan

frequency), focal bird age (positively correlated with scan frequency), focal bird sex

(males were more vigilant than females), and ambient temperature at the time of the

sample (negatively correlated with scan frequency). Because the top model was not well

supported, model averaging was used to include all variables required to describe 95% of

the variation in scan rate accounted for by the examined dependent variables. This

brought in two variables not included in the top model: the number of aggressive

interactions received from conspecifics by the focal bird and the total number of condors

socialized to the focal bird pre-fledge, essentially including all variables in the global

model. The need to include all variables to capture 95% of the variation in scan rate was

influenced by review of the literature for vigilance cues in other species and extensive

observation of condors prior to data collection. While much variation remains

unexplained, the small change in AIC_c from the top model to the global model of only

0.169 indicated that each variable examined had a small, but observable, effect on condor

vigilance. It is likely that influences on condor vigilance are many and complex, and that

a fuller picture may be obtained with much additional research time and effort. The need

to sum the AIC_c weight of the global model with the AIC_c weights of multiple other

18

models to achieve 0.95 was also likely reflective of interactive effects amongst various combinations of the examined variables. An investigation of such interactions may reveal additional variation in condor scan rate and is discussed later.

The decrease in vigilance observed as the number of condors at the site increased was not surprising, as this effect is well known in other flocking and herding species. This group size effect has been extensively investigated in other studies, and current foci of such analyses relate to the spatial dynamics of the group and the effects of aggression and scrounging behavior within the group (Burger et al. 2000, Beauchamp 2001 and 2003, Arenz 2003, Di Blanco and Hirsh 2006, Dias 2006, Fernández-Juricic and Beauchamp 2008). In the case of condors feeding at a carcass, there is a dense, core of individuals at the carcass itself and a more dispersed group of birds on the ground in the carcass area not actively feeding. This is a unique situation and, at this time, no such spatial distribution pattern has been discussed, as it relates to vigilance, in the literature. This spatial pattern offers interesting avenues of investigation for contribution to the growing body of research related to vigilance and spatial group dynamics. Scrounging (stealing of food items between feeding individuals) is common among condors. Scrounging effects, such as scanning for scrounging neighbors, should limit decreases in vigilance as group size increases (Beauchamp 2001). That group size changes produced so pronounced an effect indicated that the scrounging effects were relatively small, the cost benefit trade-off realized in increased foraging efficiency was great, or that aggression level correlates with group size and the need for conspecific, anti-aggression vigilance in large groups off-sets reductions expected from scrounger effects. Initial data

screening procedures indicated that aggression was positively correlated to group size, but the relationship was weak enough that observed multicollinearity was not enough to prevent inclusion of both in models to be examined.

The negative effect of Julian date was not expected. The most likely explanation for this relates to the fact that data was collected from June to August, the best flight weather, and in turn foraging weather, available to condors on an annual basis. With the onset of late fall and early winter, storms begin to reduce the number of flight days available. Frequently, multi-day storms will prevent flight of any kind and birds will need to go for many days, or on rare occasion's weeks, without foraging. Therefore, it is likely that birds attempt to "prepare" for these leaner months with an increase in food intake as fall approaches. The possibility of caching food as many other species do is not available to condors due to the nature of their food source. Hence, increasing intake to increase fat deposition may be the next best alternative. Decreasing vigilance by reducing scan time while at an ephemeral food source to maximize food uptake is likely the best way to achieve these ends for condors.

Although both positive (Arenz and Leger 2000) and negative (Alberts 1994, Yaber and Herrera 1994, Pravosudov and Grubb 1999) relationships have been documented in the literature, previous field observations of condors, led me to expect the positive relationship observed between age and vigilance. These field observations also revealed an apparent positive relationship between age and dominance status in reintroduced condors. Some of the age effects I observed could have been as a result of multicollinearity between these two variables. As condors achieve adult breeding status,

dominance seems to be based more on individual traits and less on an individual's age (C.

West, pers. obs.). Dominance hierarchy within the "adult" age class, characterized by the

120 month maximum, was unresolved, but was unlikely to affect overall results because

of the limited number of birds in this age range (11.7% of observations). Dominance

hierarchy positions for the rest of the flock, likely followed closely to the age distribution.

As this younger portion of the flock ages, and more individuals enter the "adult" age

category and correspondingly reorganize their dominance positions, the linear

relationship between age and dominance will likely break down. As a result, future

studies focusing on vigilance will likely need to establish formal dominance hierarchies.

In some species, younger individuals have been shown to be less vigilant than older

individuals (Aviles and Bednekoff 2007). Further, it has been shown that younger

individuals may decrease their vigilance more in groups of older more experienced

individuals than in groups of same aged conspecifics (Boukhriss et. al 2007).

Results showing that males were more vigilant than females were also expected.

Within some long-lived, monogamous species that exhibit female choice in pairing, it has

been shown that males exhibiting high levels of vigilance were preferentially selected by

females as mates (Dahlgren 1990). These vigilant males will often reduce their own

intake of food in order to scan for threats while mates and young forage (Black and Owen

1989, Gauthier and Tardif 1991, Caithamer *et al*. 1996). Such male investment in a

mate's intake of food would allow an increase in female body condition which has been

shown to increase reproductive success (Sergio *et al.* 2007).

Results showing that vigilance decreased as ambient temperature increased were not expected. The opposite relationship has been shown in small songbirds. However, these studies were conducted in low temperatures (winter) where the increase in risky behavior likely maximized food intake in order to meet the metabolic demands of thermoregulation under cold, winter conditions (Pravosudov and Grubb 1995). Temperatures experienced by the birds during my study were relatively high (average 32.1° C) and vigilance levels were unlikely to be related to metabolic demand. Temperature was strongly correlated to time of day (Appendix C), which indicated that the temperature result may in fact be describing a relationship between time of day and vigilance. Mammalian predators often focus hunting activity during crepuscular and nocturnal periods, when prey species are more active/available and when stalking methods of hunting are more effective due to reduced light (Andelt and Gipson 1979, Golightly 1981, Ayres *et al.* 1986, Beier *et al.* 1995, McCain 2008). Condor vigilance behavior patterns are similar to mammalian predator activity patterns (highest in the morning and evening with the lowest point in the middle of the day). Therefore, condors may lead diurnal lifestyles not only to take advantage of improved flight conditions, but also to avoid contact with potentially dangerous mammalian predators. Adjusting vigilance to correspond with these mid-day lulls in predator activity, likely maximizes food intake when such encounters were unlikely. As temperatures increase, there is also a possibility that spoilage of meat reduces nutritional value and that condors are more likely to engage in risky behavior to maximize the intake of resources prior to this occurring. Adequate investigation of this is difficult unless bacterial flora present are

identified, as bacterial growth rates respond differently to temperature changes based on type and metabolic pathway used (Gill and Newton 1980).

Additional Variables Included In Averaged Model

An increase in vigilance as the number of aggressive interactions received increased during feeding was expected. Individuals receiving aggression during these interactions were usually the younger and less dominant birds. This would seem to indicate that birds lower in the hierarchy, and thus younger, would be more vigilant. However, as discussed above, vigilance increased with increasing dominance. It is likely that aggressive attacks between individuals were more likely when individuals were closer in the hierarchy and dominant individuals felt the need to exercise their status (Forkman and Haskell 2004, Lu 2007). Hence, closeness in dominance to others feeding, specifically being closely subordinate to other birds present, may increase a condor's vigilance due to increased likelihood of conspecific aggression. It should be noted that while this improved the overall descriptive value of this model, the 95% confidence interval for this variable included zero and exhibited high standard error when using model averaging and in all models in which it was included (Table 3).

Results indicating an increase in vigilance with an increase in the number of conspecific social mates during the pre-fledge period was not expected. In the wild, pre-fledge individuals are generally believed to be exposed only to their parents. I therefore anticipated that socialization with no more than two adult birds pre-fledge would lead to the most adaptive behavior possible. Higher vigilance is generally accepted as more

adaptive than lower vigilance, therefore, it may be that a deviation from naturalistic

rearing was beneficial in this case. Higher rates of conspecific interaction, and likely

conspecific aggression, at an early age may cause a young bird to be more vigilant. This

may provide the individual with a higher level of overall vigilance, leading to measurable

increases in this behavior post-release. Similar to the results related to conspecific

aggression, this variable was not included in the top model selected by AIC_c. However, it

was included via model averaging performed to encompass 95% of the variation amongst

all competing models. Also similar to the results related to conspecific aggression, the

95% confidence interval for this variable included zero and exhibited high standard error

when using model averaging and in all models in which it was included (Table 3).

Model Fit

Predictability indicated by my goodness of fit test seemed adequate for both my

best model and averaged model. However, randomly generated numbers within the range

of scan rates observed for all birds also showed relatively high predictability. This effect

was likely related to variation unaccounted for by my models.

Dependent Variables

Lack of significant variation in mean scan duration when examined against my

chosen independent variables, was not expected. In Elgar's (1989) review, of 58 studies

examining individual vigilance, 24 used percentage of interval scanning, 30 used a

measure of scan rate, and 4 used a measure of the inter-scan interval. It is possible that

mean scan duration, and as a result percentage of interval scanning, is tied to the amount

of time needed to adequately examine one's surroundings. Since the same feeding site

was used throughout this study, there was little change in the complexity of habitat

structure. Hence, mean scan duration would be expected to remain relatively constant. If

the mean scan duration for each individual sampled does not vary significantly across

individuals or samples, as in my case, inter-scan interval will reflect directly in the scan

frequency. Thus, either variable would be a suitable measure of vigilance. However, if

mean scan duration varies between individuals or observation sites, then separate

analyses utilizing both scan duration and inter-scan interval as independent variables

would be recommended to achieve a fuller understanding of overall vigilance drivers in

such systems.

Unaccounted Variation

Factors influencing specific behaviors are notoriously difficult to reveal in many

cases. As such, it was not entirely surprising that my study showed a relatively complex,

multi-variable model as most accurately describing scanning behavior in California

condors. For a behavioral question being examined in a field setting, the amount of

variation described by the five variables in the top model, R^2 of 0.32, was quite good.

The converse to this begs the question as to why results were not better.

Since the relationship being examined to indicate correlation and perhaps

causation was that between the independent variables and the variation in the dependent

variable, it is clear that all of the variation in the dependent variable was not described.

Therefore, it is most reasonable that not all variables influencing scanning behavior, and

in turn vigilance, were included in this analysis.

Perhaps the most obvious missing variable relates to the presence of predators in

the carcass area. Presence of predators has been shown to increase vigilance behavior

(Caraco et al. 1980, Lendrem 1984, Poysa 1987). Due to the hilly aspect of the landscape

in which observations were made and the limited view available from my observation

blind, it was impossible for me to keep an accurate account of predators. I noted calling

of golden eagles, visual observations of golden eagles and black bears at or near the site,

chorusing of coyotes, and other indicators of predators in the area (i.e. sound of snapping

of large branches indicating black bear foraging). However, I had no sense of how many

near carcass encounters I could not detect, and so chose to exclude these data from the

analysis. Another way this could have been tested would be via introduction of artificial

predators as has been used in many studies to examine the effect of predators on focal

species behavior (Marshall and Black 1992, Pravosudov and Grubb 1998, Blumstein *et

al*. 2006). However, due to the critically endangered status of California condors, and the

fact that part of the flock was comprised of parent birds with nestlings requiring food, this

level of manipulation was not possible.

Another potentially confounding variable that may have affected vigilance

behavior was presence of common ravens (*Corvus corax*). This information is likely

available on the video footage and may be investigated further. This will require going

over all sampled feeding bouts to determine if ravens are present and also going over all

field notes for confirmation. Individuals in mixed species groups have been shown to reduce vigilance rates similarly whether foraging with their own or other species (Sullivan 1984, Cords 1989, Pravosudov and Grubb 1999). The effect on vigilance levels of mixed species groups is similar to what would be expected in a larger group. Initial observations indicated that condors did not respond to turkey vulture (*Cathartes aura*) flushing behavior the same way they responded to flushing by conspecifics. It is possible that because turkey vultures consider condors a threat, and often flush due to condor activity, condors do not cue into their threat responses. Ravens often vocalize and some condor biologists believe that condors may respond to raven vocalizations as they may indicate threats in the environment (Grantham pers. comm. 2008). This effect should be targeted for further investigation.

All models used in my information theoretic analysis were additive. One exploratory attempt at construction of a model with secondary, interactive effects included was performed after the completion of initial analyses. A lower AIC_c value was obtained from this model than from the other models used. This interactive model had an only slightly improved R^2 value. Complete examination of interactive effects amongst available variables will likely result in a better explanation of variation within this system.

CONCLUSIONS

While all sources of variation influencing my study system were not determined,

it is the first look into vigilance behavior within the complex social grouping of

scavenging vultures at a carcass. My study has created a baseline by which continued

work may further clarify the complex drivers behind this one aspect of California condor

behavior. This is the first attempt at linking rearing methods used in the California

condor captive flock to post-release survival behavior. Recent work done by Walters et

al. (2008) investigating the progress of the California Condor Recovery Team, pointed

out many shortfalls within the current recovery program. One issue addressed was the

lack of formalized research within the program. This study reflects just the sort of

research required to move the conservation of this species forward. The power of

behavioral research to speak to management questions is often overlooked (Sutherland

1998, Caro 2007). It is, however, the union of apparently disparate disciplines, such as

these, that often provide the most powerful conservation tools (Black 1991). Such a

union may even provide tools powerful enough to save the most ambitious and

aggressively denounced recovery program in North America, and perhaps powerful

enough to bring back this magnificent species.

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Appendix A. Background information on study species, California condor.

Condors are large, sexually monomorphic vultures that soar in search of large carrion over ranges which may extend for hundreds of km. Vultures are highly social, possibly due to inter-species dominance hierarchies established within scavenger guilds at large carcasses (sensu Kruuk 1967, Wallace and Temple 1987), and often travel, forage, and roost in groups (Koford 1953, Snyder and Snyder 2000). Breeding pairs are socially monogamous and may form life-long pair bonds.

Concerns over declines in the California condor population prompted their protection by the state of California in 1953 and federal listing as endangered in 1967. In the 1980's, the last wild California condors were taken into captivity for breeding efforts due to fears of extinction. The California Condor Recovery Program was established to increase numbers through captive rearing and to reestablish a wild population through reintroductions (United States Fish and Wildlife Service 1996).

Since the first release in 1992, 278 California condors have been reintroduced into California, Arizona, and Mexico; 104 are dead or presumed dead and 18 are currently returned to captivity due to exhibition of poor survival skills (Grantham 2009, personal communication). Predation and malnutrition are two causes of mortality thought to be direct results of poor survival skills involving the ability to detect predators and to feed on supplemental carcasses within the social structure of released flocks. As of May 2008, 156 reintroduced, free-flying condors remain in the wild (Grantham 2009, personal communication).

37

Appendix B. Rearing methods used by California Condor Recovery Team from inception of breeding efforts to last year of this field study (1987 – 2004).

        The condor recovery team has applied adaptive management techniques in order to expedite responses to the changing needs of the program. Rearing methods, the combination of rearing regime and socialization method, have evolved with the project and have therefore produced a mixed array of individuals with different rearing backgrounds (Clark 2003, personal communication).

 Parental care in wild condors extended for about 1½ years, only allowing 1 breeding attempt every other year. In captivity, aviculturalists found that removing eggs from nests stimulated re-laying and could increase productivity from 1 to 2 or 3 single egg clutches per year, a technique commonly referred to as multiple-clutching (Snyder and Snyder 2000). All condor eggs laid in captivity are taken for artificial incubation the first time both adults vacate the nest box simultaneously (Sterner 2003, personal communication). When the last egg to be produced for the season is laid, it is replaced with a dummy egg to perpetuate incubation behavior by the parents. Dummy eggs are eventually replaced with real eggs, either the pairs own or a foster egg, just prior to shell pipping (Levites 2003, personal communication). The pair will then incubate the egg to hatch and "parent-rear" the chick themselves in captivity. Additional eggs produced via multiple-clutching, may be fostered at shell pipping to Andean condors for parent rearing by replacement with the Andean pairs actual or dummy egg, or "puppet-reared" by humans fitted with a condor- head hand-puppet (Levites 2003, personal communication).

Appendix B. Rearing methods used by California Condor Recovery Team from inception of breeding efforts to last year of this field study (1987 – 2004) (continued).
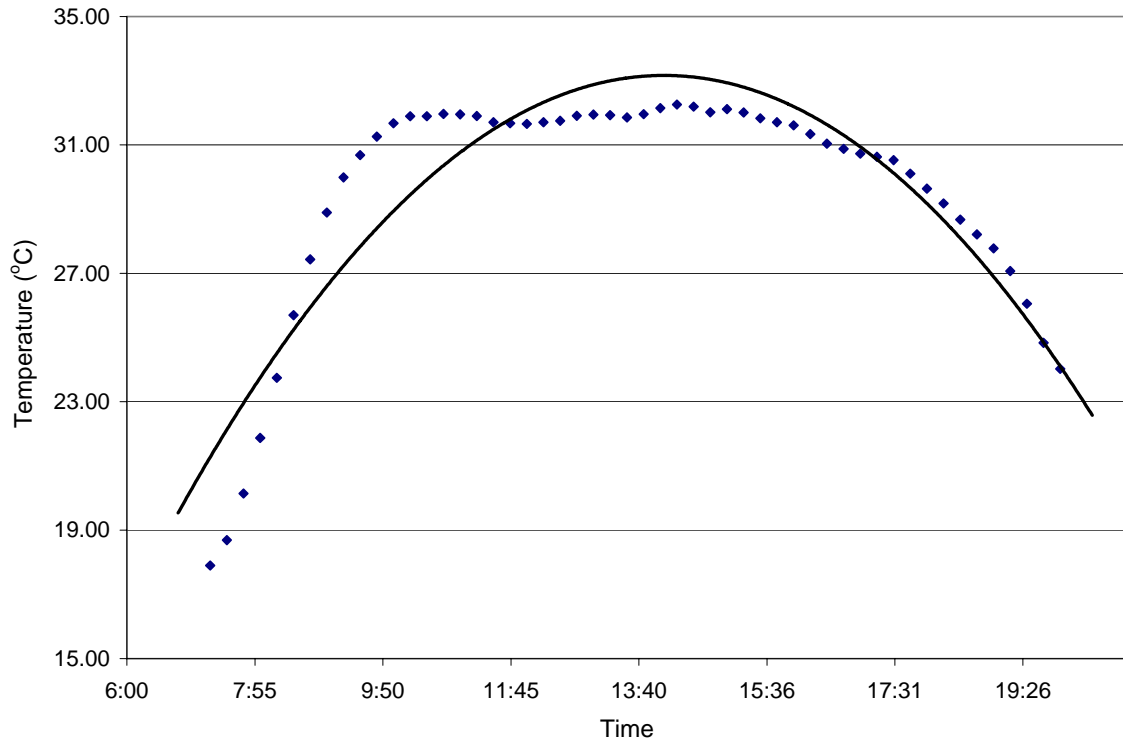
A parent-reared chick's rearing regime begins at hatch with direct rearing of chicks by parent birds. The chicks will fledge into the flight pen from the nest box when they are ready, usually at approximately six months of age (Clark 2003, personal communication). Socialization methods progresses from naturalistic socialization with parents, to removal from their parent's pen after fledge age (six months) for introduction to groups of same age conspecifics (Heinrich 2003, personal communication). Often these groups comprise release cohorts which will subsequently be released together and have older "mentor" birds included in the pens with them to help develop social skills required for integration into wild groups post-release (Heinrich 2003, personal communication, Snyder and Snyder 2000).

The rearing regime of a puppet-reared chick involves a move to an isolette chamber after hatching where they are raised with a condor hand-puppet until several months old (Snyder and Snyder 2000). Beyond the early socialization with the puppet, socialization methods used with puppet-reared chicks have varied widely (Clark 2003, personal communication). Early in the breeding program, chicks were often housed in groups after removal from isolettes and were often very aggressive toward puppets, which were passive toward the chicks and used primarily for feeding (Clark 2003, personal communication). Recently, puppet behavior has been modified to be more aggressive with individually penned chicks in order to portray the puppets as

Appendix B. Rearing methods used by California Condor Recovery Team from inception of breeding efforts to last year of this field study (1987 – 2004) (continued).

domineering figures that can subdue an aggressive chick and even initiate submissive behavior (Clark 2003, personal communication, Levites 2003, personal communication). Nearing fledge age, each chick is moved to a fledge chamber, where it may observe an adult, male, California condor mentor in an exterior pen, through mentor observation windows, and puppet care can continue; when ready, it is allowed to fledge into the exterior pen to socialize with the mentor (Clark 2003, personal communication).

Appendix C. Averaged, fifteen-minute temperature groupings; inclusive of all recorded temperatures at the condor feeding site on Hopper Mountain Wildlife Refuge in Ventura County, California from June, July, and August of 2003 and 2004. Included observations were bounded within the daily condor feeding activity window of sampled observations (07:10-19:54). Total number of temperature observations within the daily condor feeding activity window was 10,190. Effective n = 52. r^2 = 0.8445.