4-2020

An Analysis of Social Dominance in the Feeding of Ex Situ Humboldt Penguins (Spheniscus humboldti)

Robert Gabel
University of Nebraska - Lincoln

An Analysis of Social Dominance in the Feeding of Ex Situ Humboldt Penguins (*Spheniscus humboldti*)

An Undergraduate Honors Thesis
Submitted in Partial fulfillment of
University Honors Program Requirements
University of Nebraska-Lincoln

By
Robert Gabel, BS
Fisheries and Wildlife
College of Agricultural Science and Natural Resources

April 28, 2020

Faculty Mentor:
Dr. Larkin Powell, PhD, MS, BS, College of Agricultural Sciences and Natural Resources

Abstract

In the field of ecology, complex social structures, including dominance hierarchies, have been demonstrated in a variety of fauna, including bird species. While wild Humboldt Penguins (*Spheniscus humboldti*) do not exhibit a feeding hierarchy, captive penguins are under very different conditions. Humboldt penguins feed on schooling fish in the wild, but in captivity are hand fed from a zookeeper. I investigated whether there is a nonrandom pattern of dominance in the feeding order of the penguins at the Lincoln Children's Zoo, in Lincoln, NE, USA. Using a camera and tripod, with assistance from four of the zookeepers, I recorded 32 penguin feedings. I then used an Analysis of Variance (ANOVA single factor function in excel) to look for the variance amongst the mean number of fish eaten. I only ranked the penguins for the first nine fish of each feed, because there are nine penguins, thus if it was truly random they should each have averaged one fish per the first nine. I performed this analysis on all 32 feeds, but also ran it in smaller groupings based on the time of the feed (AM/PM), the weather (sunny/cloudy), and the keeper feeding (of four options), to try and account for potential bias or extra factors. The overall analysis of 32 feeds was statistically significant ($F = 13.46$, $df = 8, 279$, $P < 0.001$), and its results were backed up by the majority of the other nine analyses. Only one was not statistically significant, but was close ($P = 0.067$), and still supported the results of the overall analysis. Two penguins were found to be more dominant, having eaten on average, much more of the fish of the first nine, and two penguins were found to be more submissive. The dominant ones were a male and a female, the male being the largest penguin in the colony. The two submissive were also a male and a female, both of whom were the smallest in the colony. Neither the dominant nor submissive penguins were pair bonded with each other. This indicates

that there is a social structure in captivity, and could have implications for husbandry of Humboldt penguins, perhaps in a manner that decreases fighting during feeds. Future study should look at agonistic behavior, instead of average numbers of fish, to determine if it supports the results of this study.

Key Words: Ecology, Behavior, Humboldt penguin, *Spheniscus humboldti*

Appreciation

I would like to thank Professors North and Ferraro for participating in my thesis defense panel. I would also like to thank the Lincoln Children's Zoo for allowing me to perform my study on their penguins, and especially Keepers Baller, Erixon, Lanphier, and Wilbanks, for helping me obtain the recordings of the feedings. Finally, I want to thank my advisor, Dr. Larkin Powell, who made this whole thing possible.

Introduction.

In the study of ecology, it is important to note that the interactions between individuals of the same species can be very complicated. Organisms with complex social structures will often have dominance hierarchies, in which each individual will have some level of dominance in relation to other individuals in the group, due to competition for limited resources (Strauss, Holekamp, and Jackson, 2019). These dominance structures have been demonstrated numerous times, across a variety of fauna, including birds. For example, the Great Tit (*Parus major*) shows a correlation between social dominance and how adventurous their "personality" is (Bibi et. al. 2019). Others, such as the Striated Caracara (*Phalcoboenus australis*) will show social dominance between members of their own species as well as in competition with members of other scavenging raptor species in the Falkland Islands (Dwyer and Cockwell 2011). Across small passerines to large meat-eating scavengers, social dominance is frequent in the wild.

Is it then possible that this sort of pattern is also present in captive penguin species? Humboldt penguins are a warm weather penguin species native to the coast of South America. They are currently listed as vulnerable due to the threat of overfishing of prey resources, and ongoing climate change (BirdLife International 2018). Ex situ populations can be used to educate the public about conservation efforts and bolster wild populations through reintroductions. This brings us to the question of social dominance in captive Humboldt penguins. In the wild, they feed on commercial schooling fish depending on the geography of the colony. Some colonies rely on garfish (*Schomberesox saurus*) while others rely on anchovy (*Engraulis ringens*) or silverside (*Odontesthes regia*) to fulfill their nutritional needs (Herling et. al. 2005). This data show that a variety of fish can be used to feed and care for Humboldt penguins in captivity. In fact, frozen thawed Capelin (*Mallotus villosus*) combined with exposure to sunlight and a

vitamin pill daily provide sufficient nutrients for healthy Humboldt penguins (Tröndle et. al. 2018). Thus, it is possible to meet their nutritional needs in captivity relatively easily, however the method of feeding is quite different than naturally occurs. Zoos and botanical gardens typically hand feed the penguins to allow the keepers to monitor the health and eating habits of each individual. Beyond the nutritional aspect, Humboldt penguins show impressive adaptability to survive large temperature swings, thermoregulating themselves with a network of capillaries in their legs and feet called the rete tibiotarsale (Kazas et. al. 2017). Despite the flexibility of diet and durability in a variety of temperatures, no introduced penguin populations of any species have survived in the wild in the northern hemisphere. Occasionally an individual or small group will appear in the wild after being transported and released by fishing vessels, such as a Humboldt penguin found in Alaska in 2002 by a fisherman. However, in captivity they have thrived, becoming one of the most common species of penguin in zoos and aquariums worldwide (Van Buren and Boersma 2007). The question becomes, under otherwise healthy conditions in captivity, with the ability to adapt physiologically to the new environment, do the feeding behaviors of the penguins adapt to the new system and result in a dominance structure?

In order to have a dominance hierarchy in their ex situ colony, we should first consider whether Humboldt penguins are able to identify individuals accurately in the first place. To the human eye, Humboldt penguins look almost identical, which is why many zoos use plastic bands on their flippers to help the staff identify them. It turns out that Humboldt penguins use other methods of identifying each other than sight. All penguins in the *Spheniscus* genus utilize vocalizations to interact and stand out from each other. These vocalizations are what gave African Black Footed penguins (*Spheniscus demersus*) their nickname, the jackass penguin. Interestingly, the others in this genus also have a similar braying call, including the Humboldt

penguins, but each call is unique to the individual penguin (Favaro et. al. 2016). They can also utilize scent markers to identify each other as kin or non-kin, whether they have encountered the new penguin's scent before or not (Coffin et al. 2011). This coupled with the size and spot pattern differences between individual penguins indicates that they are quite good at identifying each other as individuals, implying that a social dominance hierarchy is possible.

I investigated whether captive Humboldt penguins show social dominance during handfeeding. Because of the importance of intraspecific competition, especially with a single food source, I predicted that feeding order would be non-random and might be influenced by age, size and sex.

Methods.

Field data collection

I performed this study at the Lincoln Children's Zoo in Lincoln, Nebraska, with permission from curator Randy Scheer. My work with animals was approved via a special event form filed with and the University of Nebraska Institutional Animal Care Program.

To collect the behavioral data, I borrowed a tripod and a Sony CX330 digital camcorder with memory card from the University of Nebraska-Lincoln's School of Natural Resources. I provided training on the equipment for zookeepers at the Lincoln Children's Zoo. From August 18, 2019 to September 19, 2019, four zookeepers recorded 32 penguin feedings. This required setting up the camera on the tripod and recording each feeding session. A standard feeding session opened with the keeper introducing themselves and passing out paddles for a game called "Eat That Fish" in which the audience members help the keeper's count the number of fish the penguin eats. Each paddle had a penguin's name, and the audience member needed to count each

time the keeper said the name of the penguin that ate a fish. This made watching the footage and recording the feeding order data much more accurate than watching for identifying characteristics and counting from the video. Once per week I downloaded the penguin feedings from the memory card to my laptop. After one month had passed, we had recorded 32 total penguin feedings.

Analysis

I watched the videos of the feedings and recorded the name of each penguin that ate and the order they ate in. I kept my database in a spreadsheet (Microsoft Excel). I also recorded date, the keeper feeding, the time of day (AM or PM feed), and the weather (sunny or cloudy) for each feeding (Figure 1).

Date:	19-Aug-19
AM/PM feed:	AM
Keeper Feeding:	Wilbanks
Cloudy/Sunny:	Sunny
1	Uhura
2	Hugo
3	Arnie
4	Arnie
5	Hugo

Figure 1. The recorded data from the August 19th, 2019 penguin feeding (up to the fifth fish fed out).

I then separated out the first nine fish of each feeding. Assuming that there is no dominance during feeds, then on average each penguin should be eating one fish of the first nine per day and in no particular order. Over time with no dominance behavior, each penguin would be expected to have the same mean ranking of fish eaten within the first 9 fish. I performed an analysis of variance using the ANOVA Single Factor function of excel. This analyzed the

amount of variance in the number of fish that each individual penguin ate, of the first nine fish fed out, during each feed. Due to there being nine penguins, the average number for each penguin should have been one if it was truly random. I ran the first analysis on all 32 feedings worth of data. I then ran eight more analyses of selected portions of the data, splitting them by factors such as the weather during the feed (sunny or cloudy), the AM feeds, the PM feeds, and which of the four keepers were feeding. This was to see if there was a difference in results possibly due to weather conditions, time of day, or subconscious favoring by the keeper feeding. Once the Anova was complete, I ranked the penguins in that sample by the average number of fish they ate in the first nine, from highest to lowest.

Results.

Across all 32 recorded feedings, there was a non-random pattern in the number of fish eaten of the first nine ($p < 0.001$), regardless of any other variables, such as cloudy and sunny days (both $p < 0.001$), AM and PM feeding times (both $p < 0.001$), and for three of the four keepers that fed (all three $p < 0.01$). The seven feedings by Keeper Wilbanks showed a similar pattern to the other ANOVA tests but were not quite statistically significant ($p = 0.0665$). Uhura (female) and Arnie (male) ate more fish than the other penguins in all but one of the statistically significant analyses. The sole exception was the set of five feedings by Keeper Baller, in which Soren was ranked first, followed by Arnie and Uhura (Table 8). There were also two penguins that consistently ate the fewest of the first nine fish, Doug (male) and Lillian (female). The only exception to this was the set of eight feeds by Keeper Erixon, in which Pengee tied with Doug and Lillian for lowest rank (Table 7).

Discussion.

The results supported my prediction, showing evidence of a non-random pattern wherein some penguins, specifically Arnie and Uhura, ate more fish at the beginning of the feed than the rest, and two other penguins Lillian and Doug, routinely ate fewer of the fish at the beginning of the feed. It would be very interesting to perform another study using the same footage, this time watching for agonistic behavior as an indicator for dominance instead and compare the results to my method of analysis. A study along those lines, using agonistic behavior in house cats (*Felis catus*) at food bowls, showed a size dominance bias wherein the larger cats were more dominant. In that same study however, age had no correlation (Knowles, Curtis, and Crowell-Davis, 2004). I also considered these factors and sex of the penguin in the results of my study.

Of the penguins, Arnie (one of the two most dominant) was at the time the heaviest penguin by half a kilogram but Uhura (the other dominant eater) was in the middle of the pack seemingly showing a weak to no size bias. On the other hand, Lillian and Doug (the two least dominant) were the two smallest penguins at the time of the study. This makes it more likely that size plays an impact, and if Uhura is considered to be an abnormal case, then there would be a clear trend. Unfortunately, my sample size and results do not allow for a rigorous conclusion with regard to the effects of size. Sex does not appear to have an impact since the most dominant and least dominant penguins were each a male and female. It should be noted that the dominant two and least dominant two are not pair bonded with each other. The results also seem to indicate that age might have an impact. As for age, Doug and Uhura are two of the three youngest penguins, all born in 2015 (Bella is the other). Arnie follows as the fourth youngest born in 2013. Finally, Lillian is the oldest penguin at the Lincoln Children's Zoo, born in 1997 (Table 1). If

Doug is considered to be an outlier, then there would be evidence that younger penguins are more dominant, however including him weakens that case.

Overall, I found some evidence to suggest that both size and age may play roles in the dominance hierarchy of the penguins as well as other possible factors that haven't been considered. Future study could help to confirm the conclusions of this research by using a traditional social dominance analysis based on agonistic behaviors. Beyond the interesting implications for the life history of captive versus wild Humboldt penguins, there is also a possible welfare benefit. It could be beneficial to study if different methods of feeding affect the levels of aggression between penguins during the feeds, and whether feeding the dominant penguins first could help decrease instances of agonistic behaviors. In theory, this could help decrease the number of injuries incurred from fighting during feeds. However, since feeding order does not impact the total number of fish each penguin receives, it is unlikely that there is a malnutrition aspect to this social dominance hierarchy.

Table 1. Individual specifics of each Humboldt penguin at the Lincoln Children's Zoo.

Penguins are listed alphabetically.

Penguin Name	Sex	Date of Hatch	Weight (kg)	Weigh Date
Arnie	Male	3/28/13	6.10	7/10/19
Bella	Female	3/25/15	5.10	7/10/19
Doug	Male	8/3/15	4.70	7/10/19
Hugo	Male	5/15/07	5.35	8/7/19
Lannie	Male	4/2/08	5.70	8/7/19
Lillian	Female	5/9/97	4.00	7/1/19
Pengee	Male	1/7/02	5.35	5/27/19
Soren	Male	1/9/02	6.05	7/1/19
Uhura	Female	3/22/15	5.05	8/7/19

Table 2. Ranking of 9 Humboldt penguins at the Lincoln Children's Zoo, Lincoln, NE, USA by the average number of fish eaten in the first nine fish eaten during each of 32 feedings (Anova Single Factor results with null hypothesis of equal means for each penguin: F = 13.46, df = 8, 279, P < 0.001).

All Feeds				
Penguin Name (Ranked High to Low)	*Count of Feeds Analyzed*	*Sum of Fish Eaten from First Nine Fed Out*	*Average Number of Fish in First Nine*	*Variance*
Uhura	32	58	1.8125	1.125
Arnie	32	56	1.75	0.96774194
Hugo	32	40	1.25	0.90322581
Soren	32	34	1.0625	0.89919355
Bella	32	33	1.03125	0.54737903
Lannie	32	24	0.75	0.70967742
Pengee	32	20	0.625	0.37096774
Doug	32	12	0.375	0.30645161
Lillian	32	11	0.34375	0.36189516

Table 3. Ranking of 9 Humboldt penguins at the Lincoln Children's Zoo, Lincoln, NE, USA by the average number of fish eaten in the first nine fish eaten during each of 17 cloudy feedings (Anova Single Factor results with null hypothesis of equal means for each penguin: F = 8.38, df = 8, 144, P < 0.001).

Cloudy Feeds				
Penguin Name (Ranked High to Low)	*Count of Feeds Analyzed*	*Sum of Fish Eaten from First Nine Fed Out*	*Average Number of Fish in First Nine*	*Variance*
Arnie	17	31	1.82352941	0.77941176
Uhura	17	31	1.82352941	0.65441176
Soren	17	21	1.23529412	1.19117647
Hugo	17	20	1.17647059	0.65441176
Bella	17	15	0.88235294	0.48529412
Pengee	17	11	0.64705882	0.49264706
Lannie	17	9	0.52941176	0.51470588
Doug	17	8	0.47058824	0.38970588
Lillian	17	7	0.41176471	0.38235294

Table 4. Ranking of 9 Humboldt penguins at the Lincoln Children's Zoo, Lincoln, NE, USA by the average number of fish eaten in the first nine fish eaten during each of 15 sunny feedings (Anova Single Factor results with null hypothesis of equal means for each penguin: F = 5.96, df = 8, 126, P < 0.001).

Sunny Feeds				
Penguin Name (Ranked High to Low)	*Count of Feeds Analyzed*	*Sum of Fish Eaten from First Nine Fed Out*	*Average Number of Fish in First Nine*	*Variance*
Uhura	15	27	1.8	1.74285714
Arnie	15	25	1.66666667	1.23809524
Hugo	15	20	1.33333333	1.23809524
Bella	15	18	1.2	0.6
Lannie	15	15	1	0.85714286
Soren	15	13	0.86666667	0.55238095
Pengee	15	9	0.6	0.25714286
Doug	15	4	0.26666667	0.20952381
Lillian	15	4	0.26666667	0.35238095

Table 5. Ranking of 9 Humboldt penguins at the Lincoln Children's Zoo, Lincoln, NE, USA by the average number of fish eaten in the first nine fish eaten during each of 18 morning feedings (Anova Single Factor results with null hypothesis of equal means for each penguin: F = 8.18, df = 8, 153, P < 0.001).

AM Feeds				
Penguin Name (Ranked High to Low)	*Count of Feeds Analyzed*	*Sum of Fish Eaten from First Nine Fed Out*	*Average Number of Fish in First Nine*	*Variance*
Uhura	18	35	1.94444444	1.46732026
Arnie	18	31	1.72222222	1.15359477
Hugo	18	23	1.27777778	1.03594771
Soren	18	20	1.11111111	1.16339869
Bella	18	16	0.88888889	0.33986928
Lannie	18	16	0.88888889	0.81045752
Pengee	18	11	0.61111111	0.36928105
Doug	18	6	0.33333333	0.23529412
Lillian	18	4	0.22222222	0.18300654

Table 6. Ranking of 9 Humboldt penguins at the Lincoln Children's Zoo, Lincoln, NE, USA by the average number of fish eaten in the first nine fish eaten during each of 14 afternoon feedings (Anova Single Factor results with null hypothesis of equal means for each penguin: F = 5.57, df = 8, 117, P < 0.001).

PM Feeds				
Penguin Name (Ranked High to Low)	*Count of Feeds Analyzed*	*Sum of Fish Eaten from First Nine Fed Out*	*Average Number of Fish in First Nine*	*Variance*
Arnie	14	25	1.78571429	0.7967033
Uhura	14	23	1.64285714	0.7967033
Bella	14	17	1.21428571	0.41758242
Hugo	14	17	1.21428571	0.7967033
Soren	14	14	1	0.61538462
Pengee	14	9	0.64285714	0.4010989
Lannie	14	8	0.57142857	0.57142857
Lillian	14	7	0.5	0.57692308
Doug	14	6	0.42857143	0.41758242

Table 7. Ranking of 9 Humboldt penguins at the Lincoln Children's Zoo, Lincoln, NE, USA by the average number of fish eaten in the first nine fish eaten during each of 8 feedings by Keeper Erixon (Anova Single Factor results with null hypothesis of equal means for each penguin:F = 3.15, df = 8, 63, P = 0.005).

Keeper Erixon's Feeds				
Penguin Name (Ranked High to Low)	*Count of Feeds Analyzed*	*Sum of Fish Eaten from First Nine Fed Out*	*Average Number of Fish in First Nine*	*Variance*
Uhura	8	15	1.875	0.98214286
Arnie	8	12	1.5	0.85714286
Hugo	8	11	1.375	0.26785714
Bella	8	9	1.125	0.69642857
Lannie	8	7	0.875	0.69642857
Soren	8	6	0.75	0.78571429
Doug	8	4	0.5	0.57142857
Lillian	8	4	0.5	0.28571429
Pengee	8	4	0.5	0.57142857

Table 8. Ranking of 9 Humboldt penguins at the Lincoln Children's Zoo, Lincoln, NE, USA by the average number of fish eaten in the first nine fish eaten during each of 5 feedings by Keeper Baller (Anova Single Factor results with null hypothesis of equal means for each penguin: F = 5.97, df = 8, 36, P < 0.001).

Keeper Baller's Feeds				
Penguin Name (Ranked High to Low)	*Count of Feeds Analyzed*	*Sum of Fish Eaten from First Nine Fed Out*	*Average Number of Fish in First Nine*	*Variance*
Soren	5	11	2.2	1.2
Uhura	5	10	2	0.5
Arnie	5	8	1.6	0.8
Bella	5	4	0.8	0.7
Hugo	5	4	0.8	0.2
Lannie	5	3	0.6	0.3
Pengee	5	3	0.6	0.3
Doug	5	2	0.4	0.3
Lillian	5	0	0	0

Table 9. Ranking of 9 Humboldt penguins at the Lincoln Children's Zoo, Lincoln, NE, USA by the average number of fish eaten in the first nine fish eaten during each of 12 feedings by Keeper Lanphier (Anova Single Factor results with null hypothesis of equal means for each penguin: F = 7.82, df = 8, 99, P < 0.001).

Keeper Lanphier's Feeds				
Penguin Name (Ranked High to Low)	*Count of Feeds Analyzed*	*Sum of Fish Eaten from First Nine Fed Out*	*Average Number of Fish in First Nine*	*Variance*
Arnie	12	26	2.16666667	1.06060606
Uhura	12	22	1.83333333	1.60606061
Soren	12	13	1.08333333	0.62878788
Bella	12	12	1	0.18181818
Hugo	12	12	1	0.54545455
Lannie	12	8	0.66666667	0.78787879
Pengee	12	8	0.66666667	0.24242424
Lillian	12	4	0.33333333	0.42424242
Doug	12	3	0.25	0.20454545

Table 10. Ranking of 9 Humboldt penguins at the Lincoln Children's Zoo, Lincoln, NE, USA by the average number of fish eaten in the first nine fish eaten during each of 7 feedings by Keeper Wilbanks (Anova Single Factor results with null hypothesis of equal means for each penguin: F = 1.98, df = 8, 54, P = 0.067).

Keeper Wilbanks's Feeds				
Penguin Name (Ranked High to Low)	*Count of Feeds Analyzed*	*Sum of Fish Eaten from First Nine Fed Out*	*Average Number of Fish in First Nine*	*Variance*
Hugo	7	13	1.85714286	2.47619048
Uhura	7	11	1.57142857	1.28571429
Arnie	7	10	1.42857143	0.95238095
Bella	7	8	1.14285714	1.14285714
Lannie	7	6	0.85714286	1.14285714
Pengee	7	5	0.71428571	0.57142857
Soren	7	4	0.57142857	0.28571429
Doug	7	3	0.42857143	0.28571429
Lillian	7	3	0.42857143	0.61904762

Literature Cited

Bibi, N., Wei, Y., Xu, H., Liang, J., Hussain, I., Ahmad, M. S., & Wang, H. (2019). Personality is associated with dominance in a social feeding context in the great tit. *Behaviour*, *156*(13/14), 1419–1434. https://doi-org.libproxy.unl.edu/10.1163/1568539X-00003572

BirdLife International 2018. *Spheniscus humboldti* . *The IUCN Red List of Threatened Species* 2018: e.T22697817A132605004. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22697817A132605004.en. Downloaded on 08 March 2020.

Coffin, H. R., Watters, J. V., & Mateo, J. M. (2011). Odor-Based Recognition of Familiar and Related Conspecifics: A First Test Conducted on Captive Humboldt Penguins (Spheniscus humboldti). *PLoS ONE*, *6*(9), 1–4. https://doi-org.libproxy.unl.edu/10.1371/journal.pone.0025002

Dwyer, J. F., & Cockwell, S. G. (2011). Social Hierarchy of Scavenging Raptors on the Falkland Islands, Malvinas. *Journal of Raptor Research,45*(3), 229-235. doi:10.3356/jrr-10-75.1

Favaro, L., Gili, C., Da Rugna, C., Gnone, G., Fissore, C., Sanchez, D., … Pessani, D. (2016). Vocal individuality and species divergence in the contact calls of banded penguins. *Behavioural Processes*, *128*, 83–88. https://doi-org.libproxy.unl.edu/10.1016/j.beproc.2016.04.010

Herling, C., Culik, B. M., & Hennicke, J. C. (2005). Diet of the Humboldt penguin (Spheniscus humboldti) in northern and southern Chile. *Marine Biology*, *147*(1), 13–25. https://doi-org.libproxy.unl.edu/10.1007/s00227-004-1547-8

Kazas, S., Benelly, M., & Golan, S. (2017). The Humboldt Penguin (Spheniscus humboldti) Rete Tibiotarsale – A supreme biological heat exchanger. *Journal of Thermal Biology*, *67*, 67–78. https://doi-org.libproxy.unl.edu/10.1016/j.jtherbio.2017.04.011

Knowles, R. J., Curtis, T. M., & Crowell-Davis, S. L. (2004). Correlation of dominance as determined by agonistic interactions with feeding order in cats. *American Journal of Veterinary Research,65*(11), 1548-1556. doi:10.2460/ajvr.2004.65.1548

Strauss, E. D., Holekamp, K. E., & Jackson, A. (2019). Inferring longitudinal hierarchies: Framework and methods for studying the dynamics of dominance. *Journal of Animal Ecology*, *88*(4), 521–536. https://doi-org.libproxy.unl.edu/10.1111/1365-2656.12951

Tröndle, U., Steinmetz, H. W., Rüegg, S. R., Müller, A., & Liesegang, A. (2018). UV-light and dietary vitamin D and their effects on ionized calcium and 25-OH-D plasma concentrations in captive gentoo penguins (Pygoscelis papua). *Journal of Animal Physiology & Animal Nutrition*, *102*(5), 1419–1428. https://doi-org.libproxy.unl.edu/10.1111/jpn.12941

Van Buren, A. N., & Boersma, P. D. (2007). Humboldt Penguins (Spheniscus humboldti) in the Northern Hemisphere. *Wilson Journal of Ornithology*, *119*(2), 284–288. https://doi-org.libproxy.unl.edu/10.1676/05-130.1