Underwater behavior of gentoo (*Pygoscelis papua*) penguins

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B.S. Biology

To
The Honors College
Oakland University

In partial fulfillment of the
requirements to graduate from
The Honors College

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February 15th, 2018

Abstract

Penguin underwater behavior has been difficult to observe and assess both in the wild and under human care. A study of ten gentoo (*Pygoscelis papua*) penguins located at the Detroit Zoo investigated underwater behavior from September 2016 to February 2017. In 2016, the Detroit Zoo opened the new Polk Penguin Conservation Center, a habitat with a 25-foot-deep, 326,000 gallon pool designed to improve well-being and promote species-typical behaviors. The gentoo penguins were monitored underwater using both live observation with focal animal sampling and automated temperature-depth recorders. Information was gathered from 90 hours of observation to better understand how the design of the habitat impacted the welfare of the penguins, as measured by use of space, and how often behaviors such as play and aggression occur. Key factors such as location and depth in the water, time of day, proximity to other penguins, and behavior of each penguin were recorded. The results included activity budgets that describe the most common underwater behaviors; conditions of play behaviors and feedings; and interactions with humans; and the amount of time each penguin spent in the water. These factors show how some gentoo penguins in the care of humans utilize their water space, socialize with other penguins, and how the conditions of the Polk Penguin Conservation Center promote good penguin welfare.

Introduction

Considerable research has examined behaviors of wild penguins and penguins under human care in terrestrial environments. Although penguin dives have been recorded by remote devices attached to penguins, little direct observation has been made while they are underwater both in the wild and in the care of humans (Putz and Cherel 2005), and there is a great need for the investigation of behaviors underwater. Observations of such behavior can reveal important information about penguin welfare.

The Association of Zoos and Aquariums' (AZA) Animal Welfare Committee defines animal welfare as "an animal's collective physical, mental, and emotional states over a period of time…measured on a continuum from good to poor" (Association of Zoos and Aquariums, 2018). Comparing typical behaviors seen in the wild to behaviors observed in captivity could reveal useful information about social interactions and health of captive birds. A positive indicator of welfare in penguins is the use of water despite a lack of need to forage. The AZA penguin care manual recommends that penguins have environmental enrichment and stimuli to bring penguins into the water (AZA Penguin TAG, 2014). In a zoo setting, foraging for food, swimming, and bathing are all common behaviors performed underwater. Occurrences of these and other diverse behaviors such as aggression, play, and kleptoparasitism have been shown to be indicators of welfare, although they have proven difficult to observe in the wild (Handley and Pistorius, 2015). Documenting these behaviors in penguins in a semi-natural setting could provide measures of penguin welfare.

Social interactions in penguins could be assessed through their behaviors including synchronized swimming, aggression and play behaviors, and human interactions. Feeding and

foraging behaviors were also important to assess welfare underwater. These behaviors are important indicators of penguin welfare and could be used to enhance penguin care.

Synchronous swimming is a behavior indicative of welfare because of its frequency of occurrence in the wild. Putz and Cherel (2005) suggest that group synchronization occurs naturally in the behavior of king penguins at sea, regardless of the duration of the dives. Tremblay and Cherel (1999) also suggest that synchronous behavior happens in northern rockhopper penguins in the water when they search and catch prey, because synchrony was found in shallow and deep dives, as well as in surface resting. It was also proposed that the penguins were in visual contact, because their dives matched in descent and ascent phases. However, Takahashi *et al.* (2004) found that while 24% of recorded foraging dives show that Adelie and chinstrap penguins are accompanied by another penguin, they are not interacting socially and thus are not considered to be synchronized swimming, which indicates that other factors may explain synchronized swimming in these species. Mori (1998) found that African penguins swam synchronously in cloudy weather conditions, suggesting that this behavior may be an anti-predation strategy.

Synchronized behavior is not typical among different species of penguins, so the observation of one species swimming underwater with another is of interest (Foerder *et. al.,* 2013). Observing the occurrences of synchronized swimming, the duration of dives and the species participating, could provide insights for assessing welfare in penguins in the care of humans. Displaying species-typical behaviors and feeding behaviors underwater, observing positive social interactions all positively impact welfare in a single species, therefore these behaviors among different species may also indicate good welfare (Handley and Pistorius, 2015).

Feeding, aggression, and play are natural behaviors commonly observed in penguins. Play behaviors are most common in juveniles and are thought to indicate good welfare (Held and Špinka, 2011). Behaviors during feedings are important to assess underwater as feeding and foraging behaviors are also indicators of good welfare (Bracke and Hopster 2006). High rates of aggression behaviors may link to frustration or stress and indicate poor welfare because the animal does not benefit from aggressive interactions (Bracke and Hopster 2006). Thus the occurrences of these behaviors could be important indicators of how the penguins perceive their habitat water space.

A factor important to the welfare in penguins in the care of humans is the effects of the presence of visitors and caretakers. Hosey (2008) highlighted the need for more information on these effects, as studies of penguins have yielded both positive and negative behavioral responses to humans. An immersive feature of the Penguin Center is the ability for visitors to stand close to the penguins, only separated by glass. This may have a "visitor effect" or change of behavior due to human presence (Ozella *et. al* 2015). Ozella *et al.* (2015) found that visitor presence in a nearby swimming pool reduced the number of penguins swimming until they habituated to humans at the end of the study. However, Brooking and Price (2004) found that when gentoo penguins were moved to a new habitat, human presence had no effect on time spent swimming. Alternatively, interactions with visitors may provide enrichment by visual interactions through the glass (Hosey, 2008), and changes in the amount of time spent near the glass could indicate habituation to humans in a new habitat. Assessing interactions between penguins and humans could reveal whether this is beneficial or contributes to stress, and how human presence might provide enrichment to enhance penguin welfare.

With a 326,000-gallon, 25-foot-deep pool, surrounded by glass for visitor viewing, the Polk Penguin Conservation Center at the Detroit Zoo offers the unique opportunity to witness behaviors underwater. In this study, the gentoo species was of particular interest because they are frequent swimmers, and often curiously investigate visitors while on land and in the water.

Automated monitoring of swimming behavior is desirable to assess penguin water use when they are not under observation. Several studies suggest that the use of small data loggers on the lower back of penguins do not interfere with penguin activity, and current studies at the Detroit Zoo (Allard and Fuller, 2015) have had great success with data loggers on the flippers of the subjects (Agnew *et. al*, 2013; Ludynia *et. al*, 2012).

The objectives of this study were to assess penguin welfare through social interactions and behaviors underwater. Synchronized swimming; feed, aggression, and play behaviors; and human interactions are of the most interest for assessing welfare.

A second objective of the study was to compare behavioral observations of penguins in another zoo. Multi-zoo comparisons are valuable for understanding conditions that promote good penguin welfare (Marshall *et al*., 2016). Similarities and differences in different penguin populations can indicate practices that support good penguin welfare in different habitats. To supplement the observations of gentoo penguins, a short case study was completed at the Parc Zoologique de Paris (Paris Zoo) observing how the Humboldt penguins there utilize their habitat and water space (Appendix C).

Materials and Methods

Subjects

The subjects of the study were 10 gentoo penguins under 5 years of age at the Detroit Zoo's Penguin Center: (Appendix A). 3 *Pygoscelis papua ellsworthi* (2 males and 1 female) and 7 (3 males and 4 female) *Pygoscelis papua papua*. All the penguins were moved to the Penguin Center before its opening in April 2016. Each penguin was already accustomed to wearing ID bands on their flippers, but different brightly colored bands were placed on each individual for identification underwater for the duration of the study. Each penguin is referred to by his or her number and arm band color, or a nickname acquired before the study (Appendix A).

The Polk Penguin Conservation Center at the Detroit Zoo opened in April 2016 and is home to about 80 penguins representing four species: rockhopper, macaroni, king, and gentoo. The Penguin Center's pool is 25 feet deep with a tunnel that allows for continuous swimming, maintained at 40 degrees Fahrenheit, and contains artificial plants, anemones, and starfish. The facility above water has two continuous terrestrial spaces with terrain representing South America and Antarctica, two places where the species of penguins living in the Penguin Center are found. While there is no difference in temperature between regions, the water habitat has two colored terrain tunnels representing "South America" and "Antarctica" for guests to observe the penguins underwater.

Behavioral observations

Behavioral data was collected from the underwater viewing areas in the lower level of the Penguin Center (Figure 1), using the ZooMonitor App (Ross *et. al* 2016). The order of observation of each penguin was determined by a randomized list of subjects for each time

period: early morning (8 a.m. – 10 a.m.), late morning (10 a.m. – 12 p.m.), and afternoon (12 p.m. - 4 p.m.). Using instantaneous sampling, each penguin's behavior, location, proximity to other penguins (including the species), and food and keeper presence were recorded each minute for 10 minutes according to the ethogram (Appendix B) (Altmann, 1974). From the ethogram in Appendix B, all-occurrence behaviors were recorded at any time during the 10-minute period.

Automated Monitoring of Swimming Behavior

To assess how much time is spent in the water by each penguin, at all hours of the day, data logger technology is extremely valuable. Data loggers are AAA-battery sized recorders attached to a custom-designed cradle for each penguin. For two weeks in January/February 2017, data loggers (LAT 1800L, Lotek Wireless Inc., Newmarket, Ontario) were attached to the flippers of the penguins and used to monitor presence in the water every six seconds.

Data Analysis

Using Microsoft Excel, scans from the ZooMonitor App were summarized into percent of total visible behaviors of each session of ten scans. The percent of total visible behaviors were averaged to create activity budgets for each penguin. A more detailed comparison of behaviors used the percent of visible behaviors for time in each location, synchronized swimming, surface swimming, bottom swimming, mid-depth swimming, and surface break behaviors between penguins using SPSS v.24.0 (IBM Corp, Armonk, NY). To assess differences among penguins and the time of day for the top 5 behaviors, and between locations within the habitat pool, the arcsine of the proportion of visible activities was used in a two-way ANOVA.

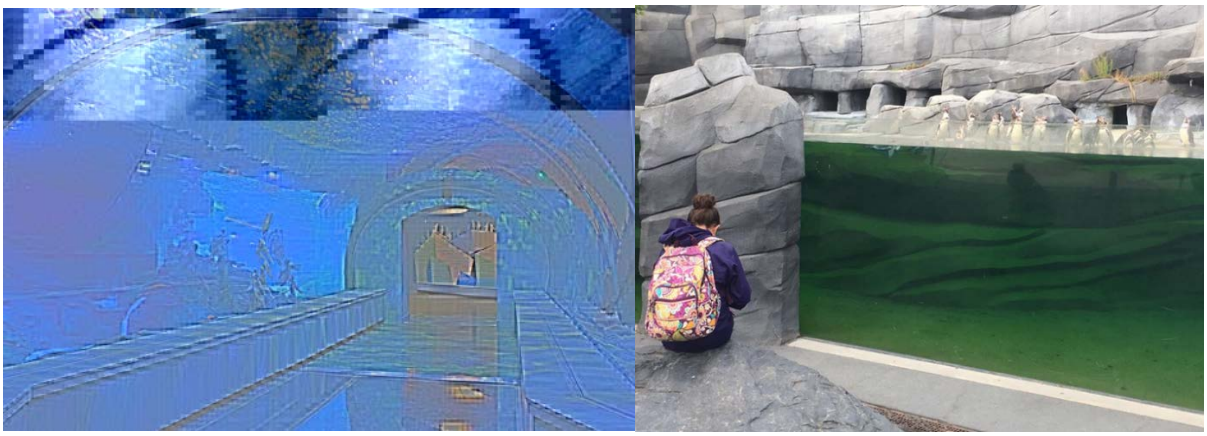


Figure 1. (Left) The South America Tunnel at the Detroit Zoo, an underwater viewing area ("Media"). While there is only one pool in the Penguin Center, it is so large that different locations were designated for the purpose of this study: the South America Tunnel, Main Pool, and Antarctica Tunnel. The Main Pool area begins across the land bridge to the left of the picture, and there is a tunnel to the right of the picture where penguins can swim to the Antarctica Tunnel, adjoining the Main Pool.

Figure 2. (Right) The Humboldt penguin exhibit at the Paris Zoo. The pool had three sides to observe the penguins, and a rocky shore on land with sheltered nesting sites. The penguins were only observed in the water.

Results

Approximately 87 hours of observational data (of both visible and not visible behavior) was collected from September 2016 to February 2017 at the Detroit Zoo.

Location

There was a significant difference in the average amount of time spent in each area by all penguins, with the most time spent in the Antarctica Tunnel ($F_{2,1179)} = 56.9$, $P < 0.001$; Fig. 3).

Automated Monitoring of Swimming Behavior

Penguins spent on average 24.7 ± 2.2% of time swimming during the two weeks they were fitted with data loggers (Fig. 4). 13607: Purple swam the most (39.6% of time), and Philly: Neon Yellow swam the least (15.5% of time).

Swimming Activities Observed

Penguins were observed participating in 21 different behaviors (Appendix B), although not all behaviors were observed in all penguins (Fig. 5). The most common behaviors included synchronized swimming, surface break, mid-depth swim, bottom swim, and surface swim, and accounted for 88% of the total average behaviors in the water.

Synchronized swimming was the most common behavior observed (18.2 ± 3.8%; range: 4.09 - 36.63% of time). There were significant differences among individuals in the proportion of time spent synchronized swimming ($F_{9,376)} = 15.3$, $P < 0.001$; Fig. 6). In addition, penguins spent a greater amount of time synchronized swimming in the afternoon than the morning (24.1 ± 5.6 % of time vs. 15.2 ± 3.0 % of time, respectively) ($F_{1,376)} = 20.3$, $P < 0.001$; Fig. 6). There was also an interaction between individual time spent synchronized swimming and the time of

day ($F_{9,376)}$ =1.9, P < 0.05; Fig. 6). Therefore, most penguins spent more time synchronized swimming in the afternoon than in the morning.

Surface swimming was observed (3.2 ± 0.28 % of time; Range: 2.13 – 5.23 % of time) without statistically significant differences among individuals (P = 0.974; Fig. 7) or the time of day of surface swimming (P = 0.20; Fig. 7). There was no interaction between individuals and time of day surface swimming occurred (P = 0.069; Fig. 7).

Average proportion of bottom swimming was the behavior least observed (1.5 ± 0.40 % of time; Range: 0 - 4.05 % of time) with statistically significant differences between individual time spent ($F_{9,376)}$ = 2.851, P = 0.003; Fig. 8). There was no significant difference in the time of day bottom swimming occurred (P = 0.433). However, there was an interaction between individual time spent bottom swimming and the time of day ($F_{9.376)}$ =3.83, P < 0.001; Fig. 8). Most penguins bottom swam in the morning as opposed to in the afternoon (1.72 ± 0.61 % of time vs. 1.35 ± 0.69 % of time, respectively).

Mid-depth swimming was observed (6.5 ± 0.65 % of time; Range: 4.17 - 10.46 % of time) with significant differences between individuals ($F_{9,376)}$ = 2.95, P = 0.002; Fig. 9). There was not a significant difference in the time of day mid-depth swimming occurred ($F_{9,376)}$ = P = 0.069; Fig. 9)

Surface break swimming was the second-most common behavior observed (16.26 ± 2.24 % of time; Range: 11.05 -31.13 % of time) with significant differences between individuals ($F_{9,376)}$ = 5.38, P < 0.001; Fig. 10) and no difference in time of day surface break swimming (P = 0.108).

Feeding, Play, and Aggression Behaviors

A summary of the number of occurrences observed of play and aggression behaviors is presented in Figure 12 and Table 1. Feedings occurred during 67 sessions recorded, and occurrences of feeding and food interaction were observed for almost every bird. Kleptoparasitism was observed 10 times in the study, with the most occurrences (four) by 13606: White, who was also the receiver of the most acts of kleptoparasitism observed (three). 146 occurrences of play behaviors- play chase and play swim- were observed. From notes during observations of Popeye and Philly, contact aggression sometimes occurred before a bout of play chase. In other penguins, bathing sometimes occurred before play swim. There were low numbers of aggression, which are a combined number of contact and non-contact aggression, and human interaction.

Human Interactions

From notes during observations, 13606: White and 13605: Blue were observed to interact with keepers and investigate objects the divers were holding while in the pool. Except for 13596: Red, 13604: Yellow, and Simon, all the penguins were observed to interact with visitors through the observation glass.

Discussion

The purpose of the study was to evaluate social interactions and behaviors underwater to assess penguin welfare of the gentoo penguins at the Detroit Zoo Penguin Center. Overall, the gentoo penguins display a wide range of water-related behaviors that indicates good welfare, including: synchronized swimming, feeding and play behaviors, and human interactions; and few occurrences of behaviors that could be negative indicators.

Location

All the penguins spent the least amount of time in the South America tunnel, which may be due to their habit of swimming laps in a clockwise direction from the South America Tunnel, to the Main Pool, to the Antarctica Tunnel, and often briefly coming to the surface in the Antarctica Tunnel. The ease of visual assessment in the water in each location may also affect where the penguins were observed. The use of all parts of the water space in the Penguin Center is a positive response to the habitat, and indicator of good welfare. There was no correlation among individual penguins and preferred depths of swimming, suggesting that the gentoo penguins are utilizing their entire water space (Fig. 5).

Automated Monitoring of Swimming Behavior

The average percent of time spent swimming during the two-week data logger study was 24.7%, which could be compared to other populations of gentoo penguins in human care, as the amount of time spent in the water is a positive indicator of penguin welfare (AZA Penguin TAG, 2014). Luna-Jorquera and Culik (1999) fitted twelve wild Humboldt penguins in Chile with data loggers for three days and reported an average 25.1 hours at sea, or 34.9 % of time at sea.

Without accounting for differences in species, the percent of time of the gentoos (24.7%) and the wild Humboldt penguins (34.9%) are similar and indicates good welfare of the gentoo penguins in the care of humans. 13607: Purple was in the water 40 % of time, the most of all the penguins, and the two gentoo subspecies swam at similar amounts (Fig. 4).

Swimming Activities Observed

The diverse behaviors portrayed in the activity budgets (Fig. 5) are indicators of positive penguin welfare. Synchronized swimming was by far the most common behavior, and the prevalence of this behavior in the Penguin Center habitat provides information about the social dynamics of the Gentoo penguins at the Detroit Zoo. While the lights in the habitat change on a schedule, the water is maintained at 40 °F, and there is no change in weather. Unlike synchronized dives observed in cloudy weather only (Mori, 1998), synchronized swimming occurred at different times of the day with no change in weather. However, it did occur more in the afternoon than in the morning (Fig. 6). Synchronized swimming also did not occur during in-water feedings, and fish are not present in the water at other times, so it may not be a hunting strategy as suggested by Tremblay and Cherel (1999), although they studied northern rockhopper penguins. There are no predators present in the Penguin Center, so there may be another social aspect to synchronized swimming that should be investigated further.

Feeding, Play, and Aggression Behaviors

There was a very low occurrence of aggression behaviors seen in the activity budgets (Fig. 5) and all occurrence behavior table (Figure 12, Table 1). Some instances of aggression between Philly: Neon Yellow and Popeye: Light Blue were seen before bouts of play swimming,

and further research should investigate any correlation between the two behaviors. Play chase and play swim were two social behaviors observed in all the penguins except for 13596: Red, and Thor: Neon Orange, who did not ever play chase (Figure 12, Table 1). The variety of play behaviors in a large number of the penguins are positive indicators of welfare. All of the penguins are below five years of age, which may also be a reason for high occurrences of play behaviors (Held and Špinka, 2011). 13606: White was observed to be the highest instigator and receiver of kleptoparasitism and further study would be needed to ascertain a correlation between these behaviors. Feeding times are also very chaotic for observation, and additional instances of kleptoparasitism may be difficult to ascertain when observing different penguins. However, other aggression was not observed during feedings in the water, which indicates that it is a husbandry practice that promotes good welfare.

Human interactions

Almost every penguin interacted with visitors through the glass underwater at least once during the study (Figure 12, Table 1). Simon, 13596: Red, and 13604: Yellow did not interact with visitors or keepers at all while underwater. From notes during observation, visitor interactions often happened with children wearing brightly colored clothing, or adults holding something up to the glass. 13606: White and 13605: Blue both had human and keeper interactions more than the other penguins, and were observed to investigate more underwater, so these occurrences might be due to a more inquisitive nature in these individuals. The occurrences seem to be positive as suggested by Hosey (2008), which indicates good welfare. Therefore, by using the Penguin Center habitat's unique underwater glass feature, enrichment is provided to the penguins that engage with the keepers or visitors.

Paris Zoo Comparison

The Paris Zoo case study only observed the Humboldt penguins when in the water and found that, similar to the gentoo penguins, they spent much of their time in the water, had diverse behaviors, and also swam in groups (Fig. 11). The high occurrences of surface swimming and break could be because the pool is not as deep as the Penguin Center pool. During observation on both days, there were rain showers, during which many of the penguins play swam and bathed. Rain has been found to reduce breeding pair numbers in Humboldt penguins in Chile, so changes in behavior could be due to the rain (Simeone *et al.* 2002). Investigation between weather and behaviors may be valuable to outdoor habitat studies in the future.

Similar to the gentoos, the Humboldt penguins had a wide variety of behaviors in the water, which indicates good welfare (Fig. 11). However, there was much less time spent observing penguins at the Paris Zoo case study than at the Detroit Zoo. Studies at different locations may be valuable to comparing habitats and husbandry practices, although difficult to complete because of the number of variables between institutions. Future studies could be done between the same species at different locations, but equal time at both locations would be valuable (Marshall *et al*., 2016).

Summary

The gentoo penguins in the Detroit Zoo Penguin Center use their water space for swimming, social interactions, and feedings—promoting high levels of these species-typical behaviors suggests the water space positively impacts their welfare. The penguins swam in the water 24.7% of their day, on average. Synchronized swimming was the most common behavior,

and seems to be a preferred social activity that every bird participates in. It may not be a hunting strategy, as it did not occur during feedings, but it is a positive indicator of good welfare (Putz and Cherel, 2005). Almost all of the penguins were observed feeding underwater, and the extremely low occurrences of aggressions, especially during in-water feedings, indicates a husbandry practice that promotes good welfare. The absence of rain and cloudy weather does not seem to have an effect on the behavior of the gentoo penguins but weather may have affected the behavior of the Humboldt penguins, and future studies on weather effects on captive birds would be valuable (Simone *et. al*, 2002). The option for human interactions in the Penguin Center also promotes good welfare, as the behavioral response of the penguins suggest these interactions are enriching for them (Hosey 2008). This study contributes to our understanding of gentoo penguin behavior and welfare and can be used to support best practice, including pool feeds, and also demonstrate the value of comparing species and habitats to understand differences and look for additional ways to help animals thrive under human care.

Acknowledgements

This project would not have been possible without my mentor from the Detroit Zoo, Dr. Matthew Heintz, and my mentor from Oakland University, Dr. Keith Berven. I would like to thank Dr. Heintz~~,~~, Dr. Grace Fuller, and Dr. Stephanie Allard of the Detroit Zoological Society Center for Zoo Animal Welfare and Ethics for their guidance throughout my thesis process. Data collection methods on ZooMonitor and analysis organization methods using Microsoft Excel for ZooMonitor and data logger data were created by Dr. Heintz and Dr. Fuller, and data was analyzed on SPSS with the help of Dr. Berven. I would also like to thank Oakland University's

Honors College for the Thesis Grant that made traveling to the Detroit Zoo and the Paris Zoo for this study possible.

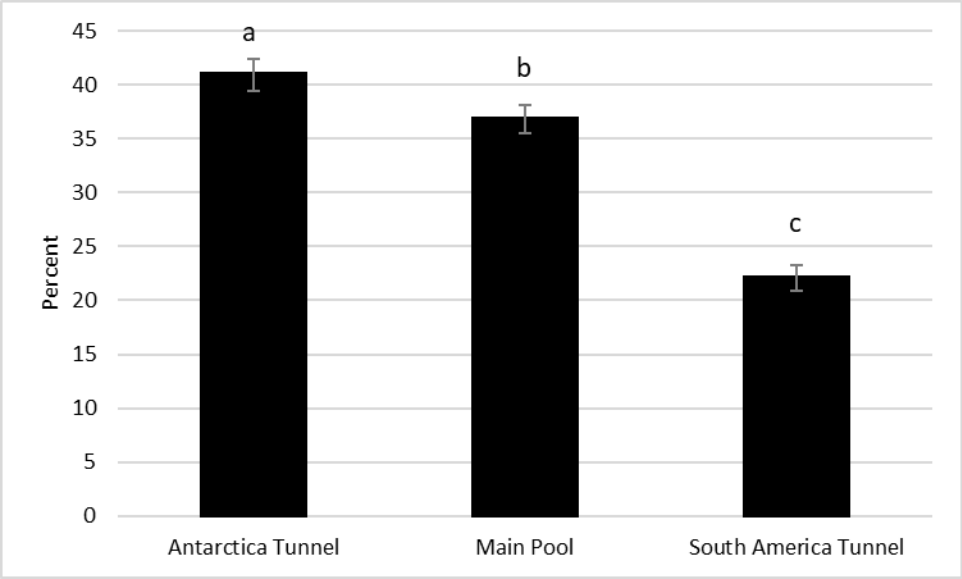


Figure 3. Total average time (% of total time observed) spent in each location underwater ((a) Antarctica Tunnel, (b) Main Pool, and (c) South America Tunnel) by all Detroit Zoo gentoo penguins (n = 10).

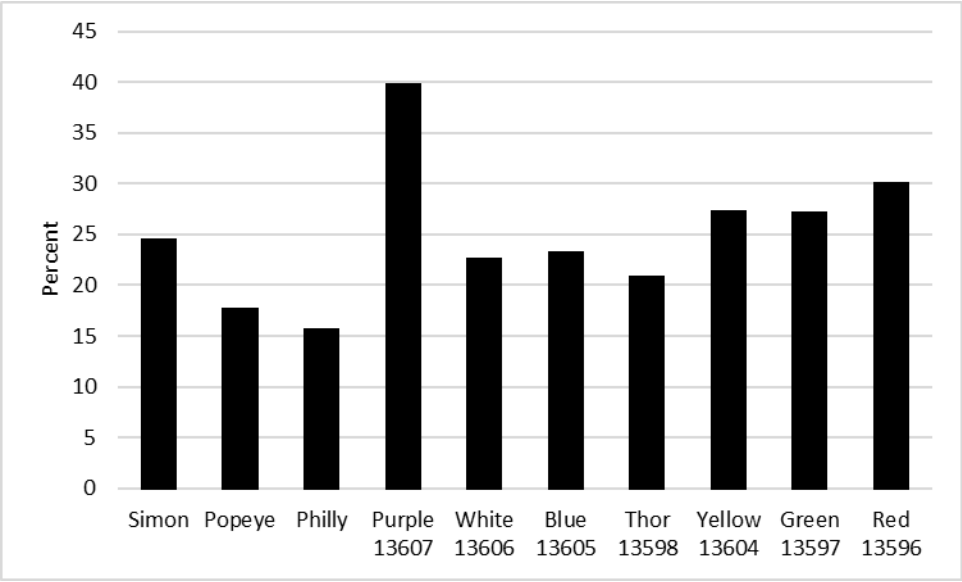
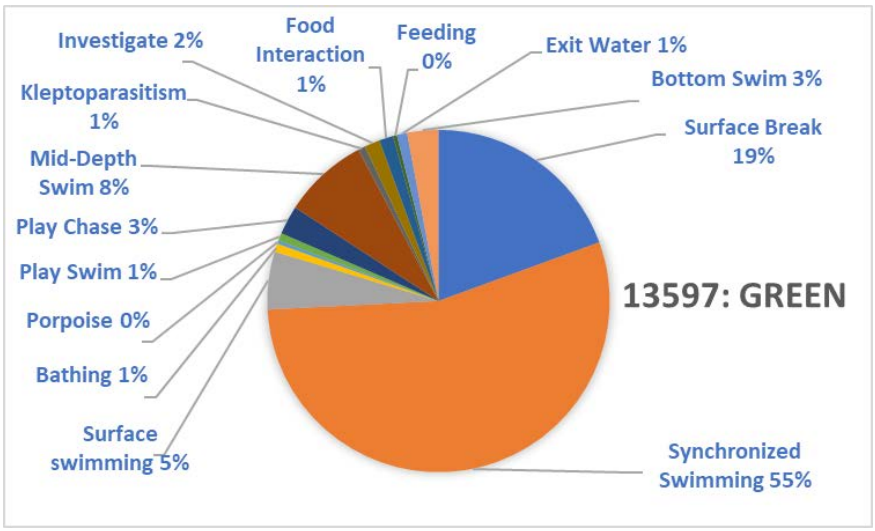
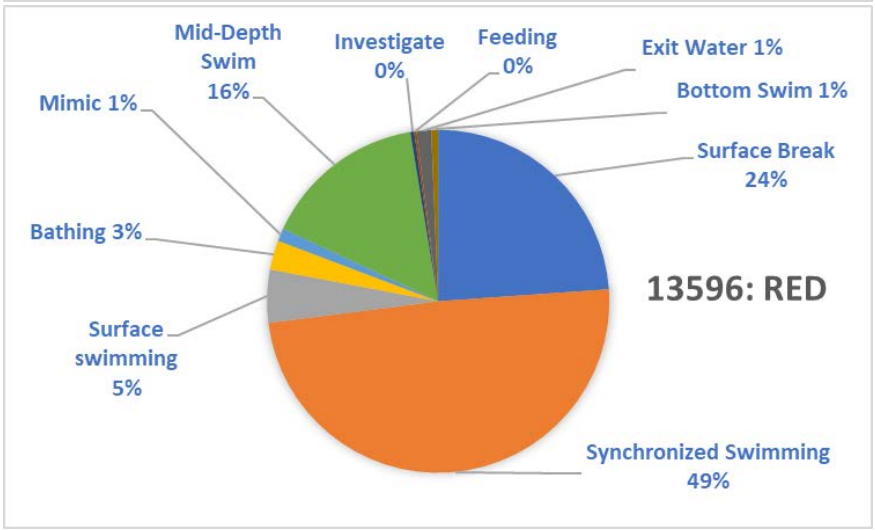
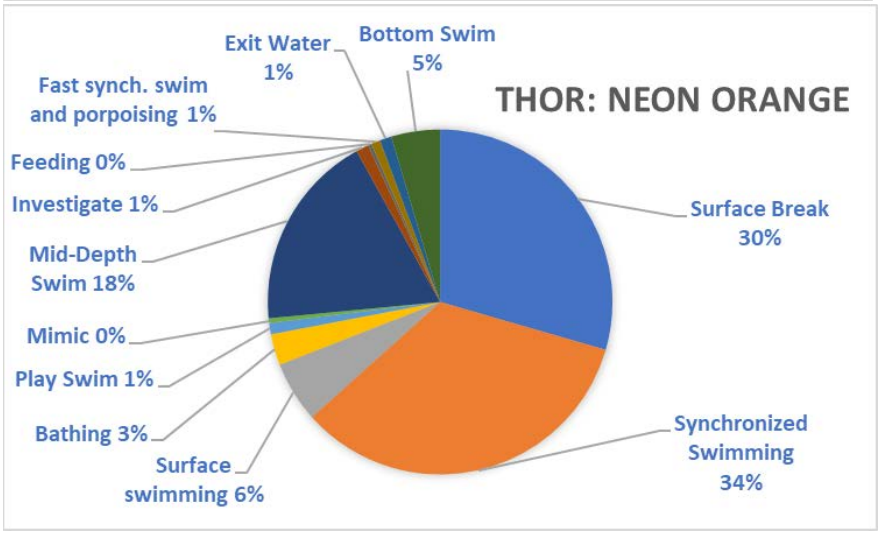
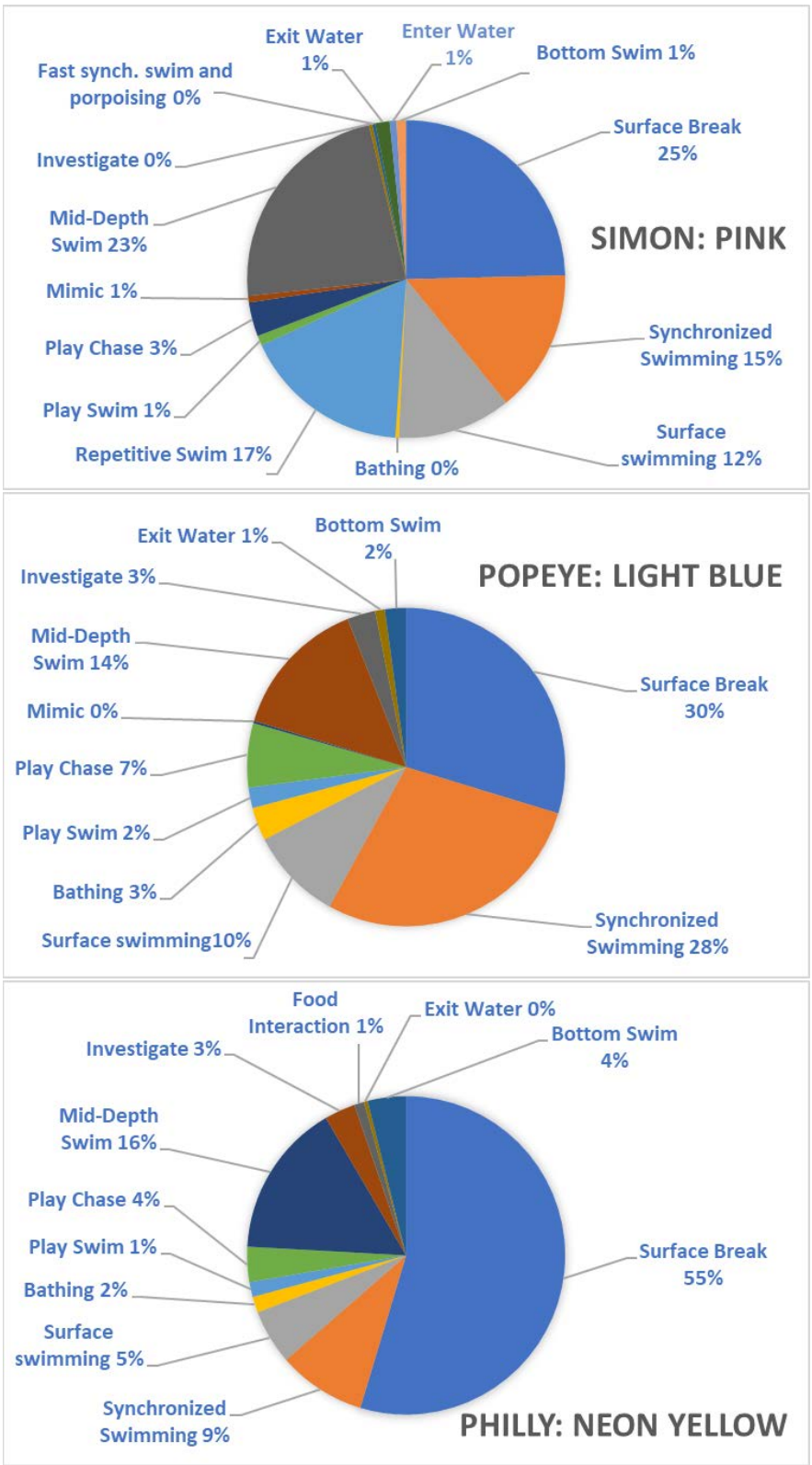


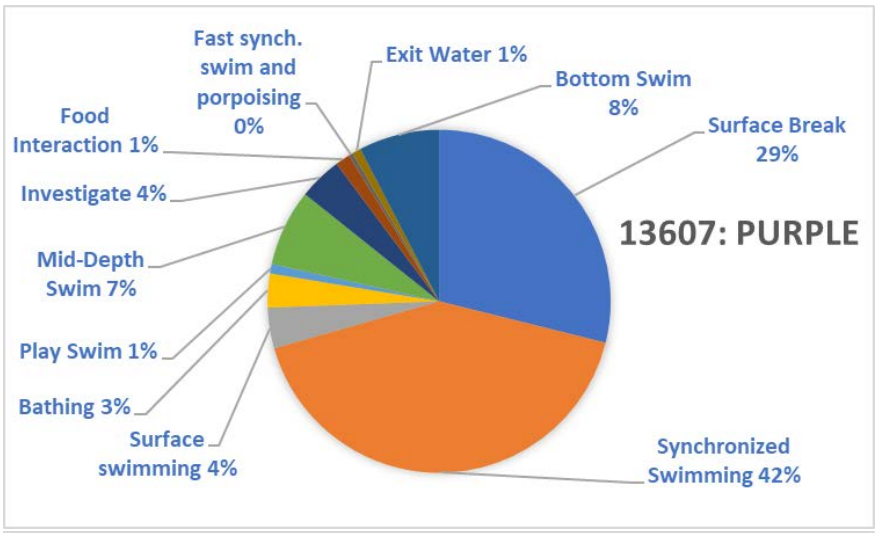
Figure 4. Total percent of time spent swimming for each Detroit Zoo gentoo penguin (n =10), analyzed from data logger recorded data.

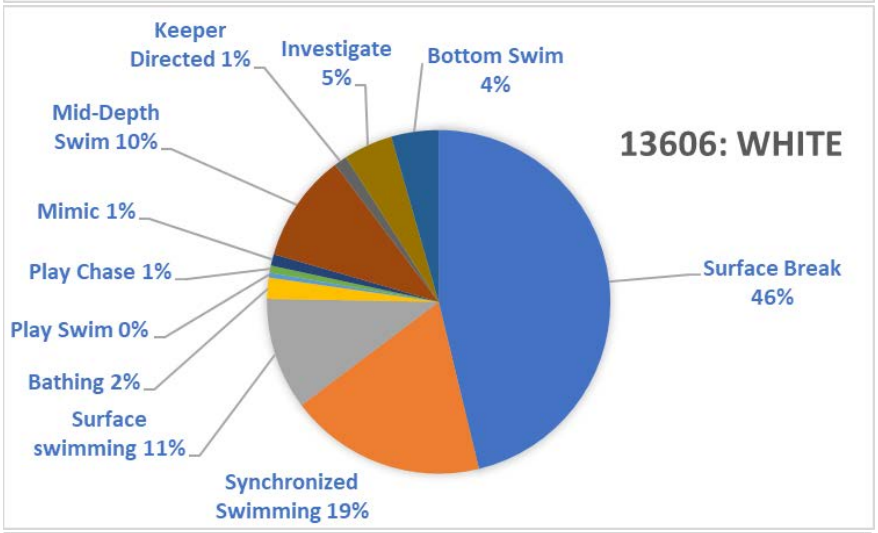

Investigate 2%
Food Interaction 1%
Feeding 0%
Exit Water 1%
Bottom Swim 3%
Kleptoparasitism 1%
Surface Break 19%
Mid-Depth Swim 8%
Play Chase 3%
Play Swim 1%
Porpoise 0%
Bathing 1%
Surface swimming 5%
Synchronized Swimming 55%
13597: GREEN

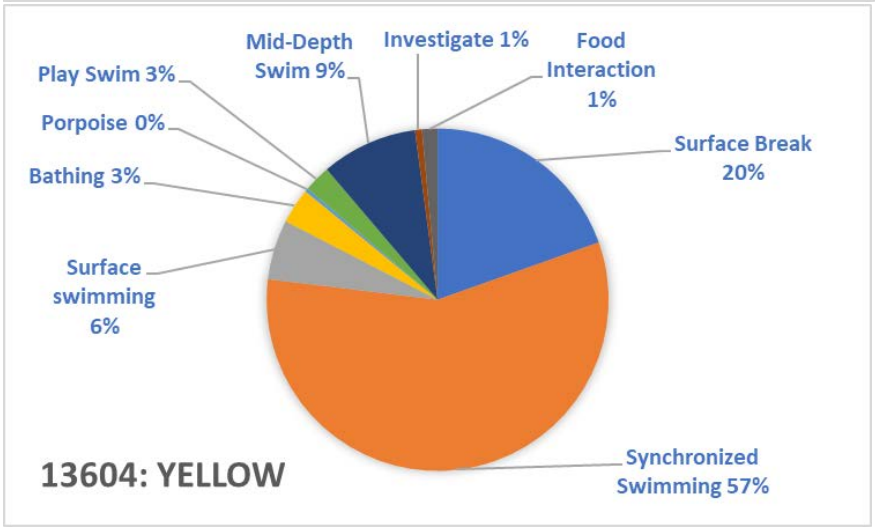

Mid-Depth Swim 16%
Investigate 0%
Feeding 0%
Exit Water 1%
Bottom Swim 1%
Mimic 1%
Surface Break 24%
Bathing 3%
Surface swimming 5%
Synchronized Swimming 49%
13596: RED


Exit Water 1%
Bottom Swim 5%
THOR: NEON ORANGE
Fast synch. swim and porpoising 1%
Feeding 0%
Surface Break 30%
Investigate 1%
Mid-Depth Swim 18%
Mimic 0%
Play Swim 1%
Synchronized Swimming 34%
Bathing 3%
Surface swimming 6%


Exit Water 1%
Enter Water 1%
Bottom Swim 1%
Fast synch. swim and porpoising 0%
Surface Break 25%
Investigate 0%
Mid-Depth Swim 23%
SIMON: PINK
Mimic 1%
Synchronized Swimming 15%
Play Chase 3%
Play Swim 1%
Surface swimming 12%
Repetitive Swim 17%
Bathing 0%
Exit Water 1%
Bottom Swim 2%
Investigate 3%
POPEYE: LIGHT BLUE
Mid-Depth Swim 14%
Surface Break 30%
Mimic 0%
Play Chase 7%
Play Swim 2%
Bathing 3%
Synchronized Swimming 28%
Surface swimming10%
Food Interaction 1%
Exit Water 0%
Bottom Swim 4%
Investigate 3%
Mid-Depth Swim 16%
Play Chase 4%
Surface Break 55%
Play Swim 1%
Bathing 2%
Surface swimming 5%
Synchronized Swimming 9%
PHILLY: NEON YELLOW


Fast synch. swim and porpoising 0%
Exit Water 1%
Bottom Swim 8%
Food Interaction 1%
Surface Break 29%
Investigate 4%
13607: PURPLE
Mid-Depth Swim 7%
Play Swim 1%
Bathing 3%
Surface swimming 4%
Synchronized Swimming 42%


Keeper Directed 1%
Investigate 5%
Bottom Swim 4%
Mid-Depth Swim 10%
13606: WHITE
Mimic 1%
Surface Break 46%
Play Chase 1%
Play Swim 0%
Bathing 2%
Surface swimming 11%
Synchronized Swimming 19%


Mid-Depth Swim 9%
Investigate 1%
Food Interaction 1%
Play Swim 3%
Porpoise 0%
Surface Break 20%
Bathing 3%
Surface swimming 6%
Synchronized Swimming 57%
13604: YELLOW

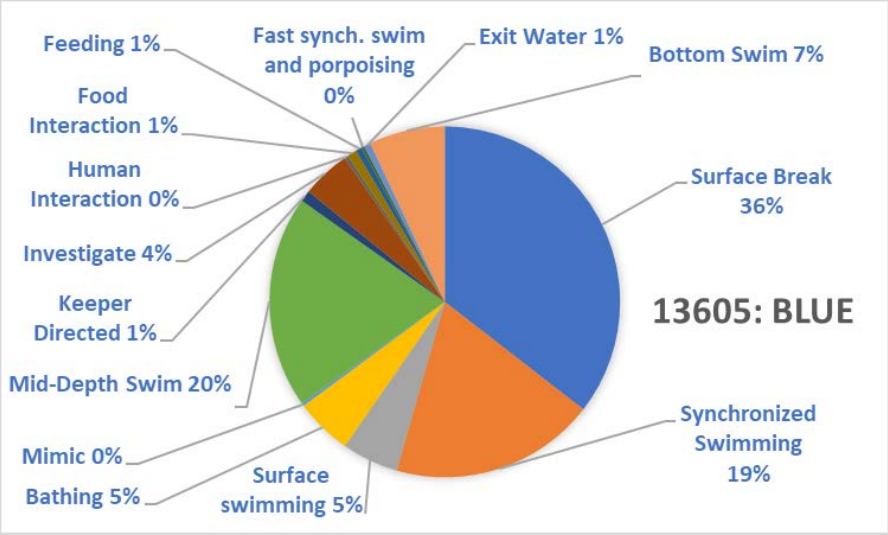


Figure 5. Activity budgets out of all visible behaviors of each Detroit Zoo gentoo penguin.

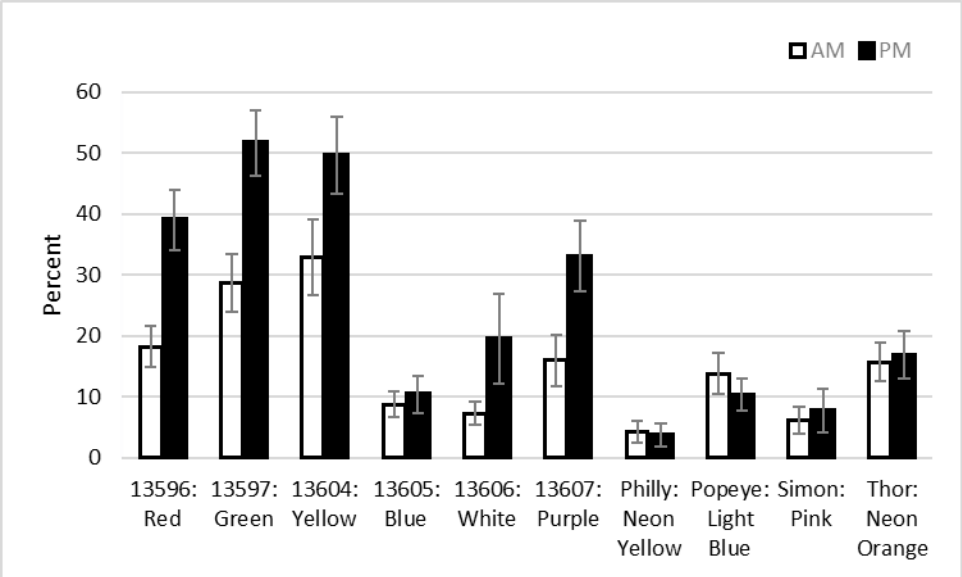


Figure 6. Average of percent synchronized swimming for each Detroit gentoo penguin (n = 10). There were significant differences among individuals in the proportion of time spent synchronized swimming ($F_{9,376)} = 15.3$, $P < 0.001$). In addition, penguins spent a greater amount of time synchronized swimming in the afternoon than the morning (24.1 ± 5.6 % of time vs. 15.2 ± 3.0 % of time, respectively) ($F_{1,376)} = 20.3$, $P < 0.001$). There was also an interaction between individual time spent synchronized swimming and the time of day ($F_{9,376)} = 1.9$, $P < 0.05$).

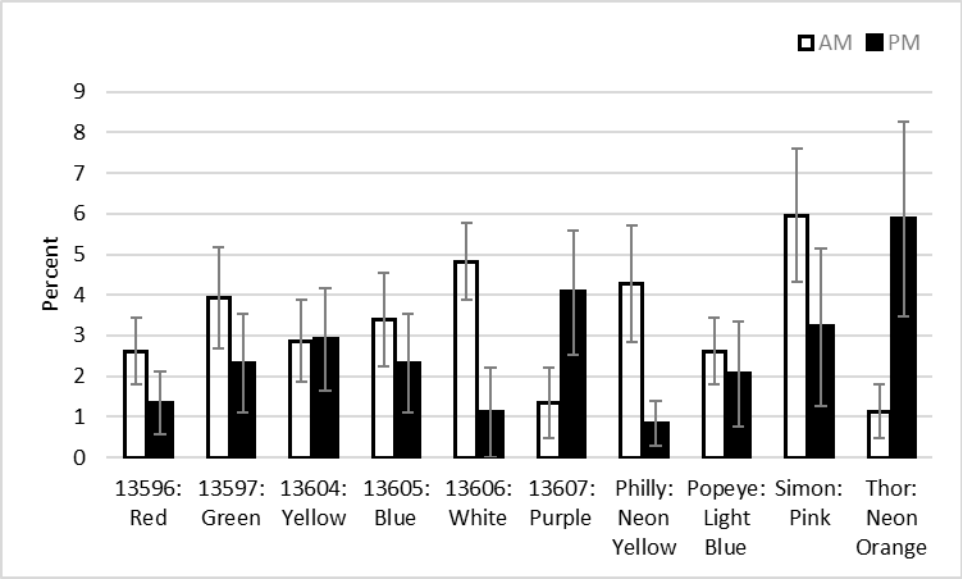


Figure 7. Average of percent surface swim for each Detroit gentoo penguin (n = 10). Surface swimming had no statistically significant differences among individuals (P = 0.974) or the time of day of surface swimming (P = 0.20). There was no interaction between individuals and time of day surface swimming occurred (P = 0.069).

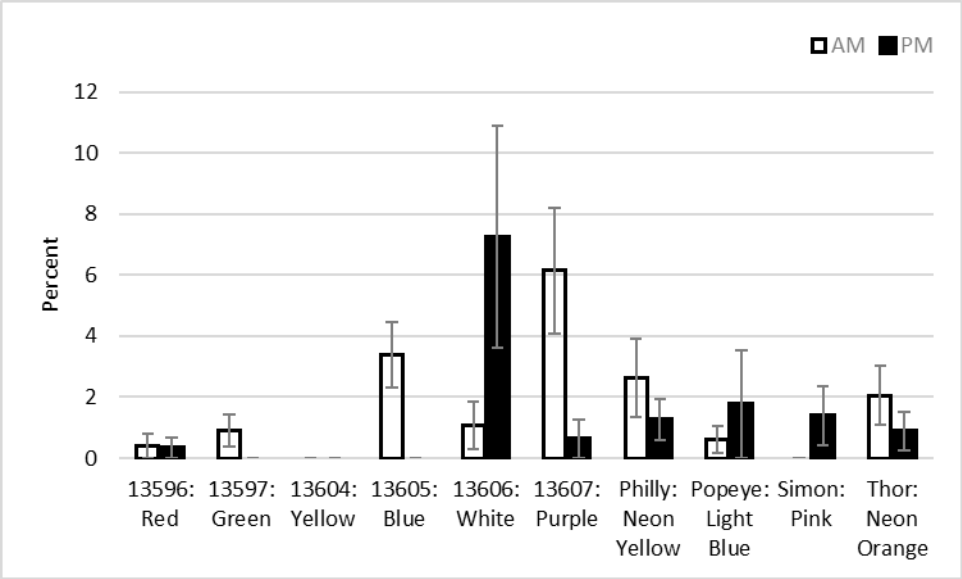


Figure 8. Average of percent bottom swim for each Detroit gentoo penguin (n = 10). There were statistically significant differences between individual time spent bottom swimming ($F_{9,376)}$ =

2.851, P = 0.003). There was no significant difference in the time of day bottom swimming occurred (P = 0.433). However, there was an interaction between individual time spent bottom swimming and the time of day ($F_{9.376)}$ =3.83, P < 0.001). Most penguins bottom swam in the morning as opposed to in the afternoon (1.72 ± 0.61 % of time vs. 1.35 ± 0.69 % of time, respectively).

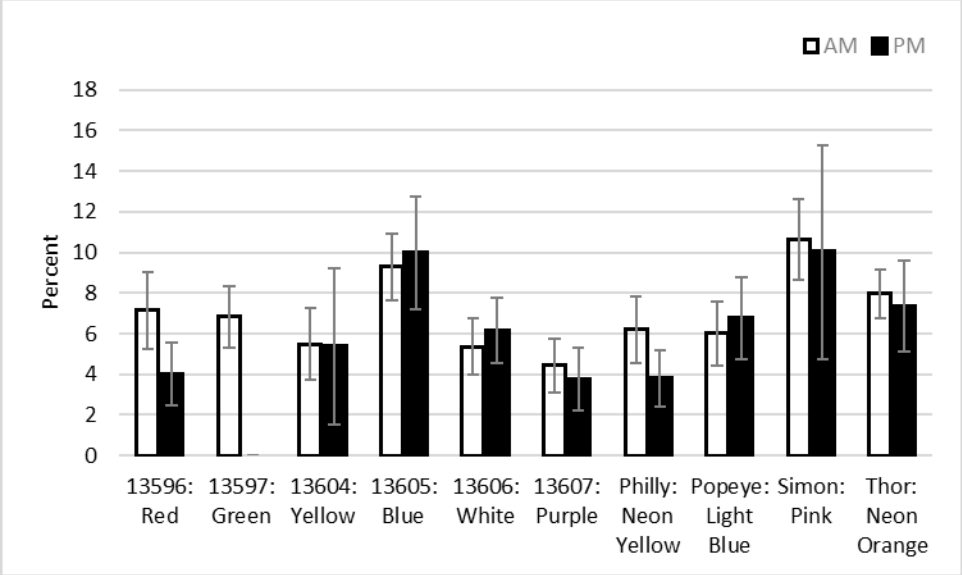


Figure 9. Average of percent mid-depth swim for each Detroit gentoo penguin (n = 10). There were significant differences between individuals ($F_{9,376)}$ = 2.95, P = 0.002), but no significant difference in the time of day mid-depth swimming occurred ($F_{9,376)}$ = P = 0.069).

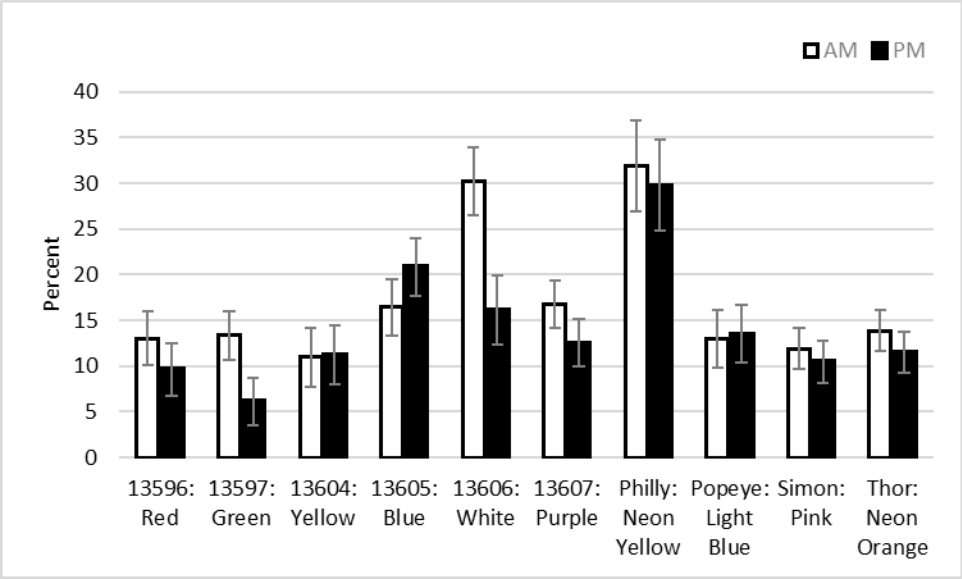


Figure 10. Average of percent surface break for each Detroit gentoo penguin (n = 10).

There were significant differences between individuals ($F_{9,376)} = 5.38$, $P < 0.001$) and no difference in time of day surface break swimming ($P = 0.108$).

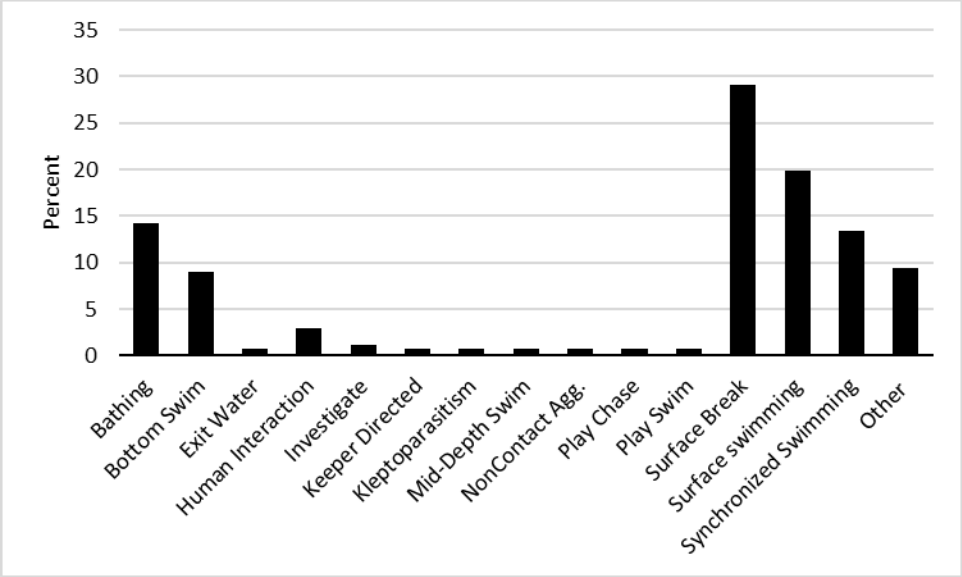
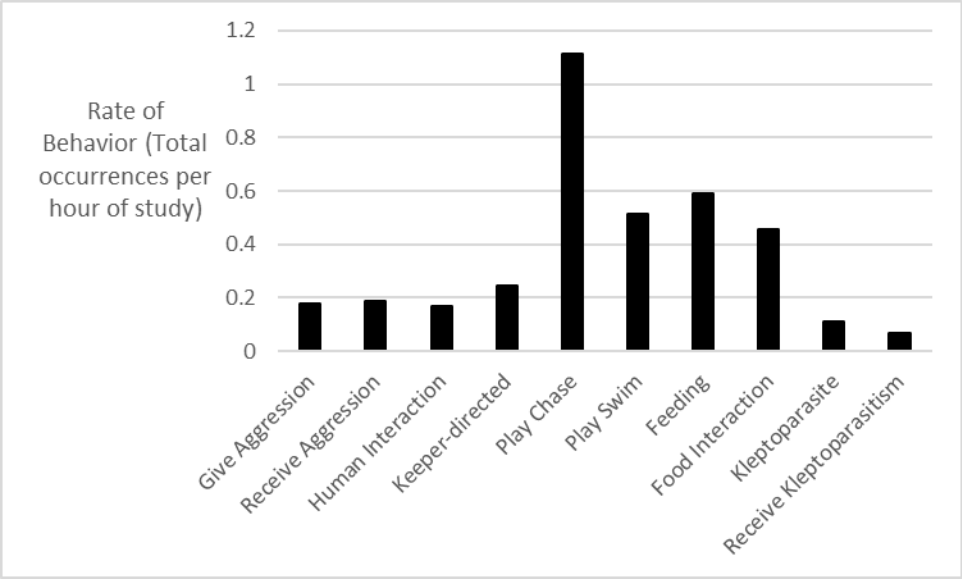


Figure 11. The total percent of average activities of the Humboldt penguins at the Paris Zoo (n = 16).



Row Labels	Give Aggression	Receive Aggression	Human Interaction	Keeper-directed	Play Chase	Play Swim	Feeding	Food Interaction	Kleptoparasite	Receive Kleptoparasitism
13596: Red	0	0.02	0	0	0	0	0.03	0	0	0
13597: Green	0.02	0.01	0.03	0.01	0.02	0.02	0.14	0.14	0.03	0.01
13604: Yellow	0	0	0	0	0.01	0.09	0.11	0.01	0	0
13605: Blue	0.01	0	0.04	0.09	0.02	0	0.08	0.08	0.01	0
13606: White	0.01	0.02	0.03	0.13	0.08	0.03	0.02	0.01	0.04	0.03
13607: Purple	0	0.01	0.01	0	0.04	0.02	0.01	0.09	0.01	0
Philly: Neon Yellow	0.07	0.04	0.01	0	0.23	0.09	0.09	0.07	0	0.02
Popeye: Light Blue	0.03	0.06	0.01	0.01	0.46	0.13	0	0	0	0
Simon: Pink	0.03	0.02	0	0	0.24	0.09	0.04	0.02	0.01	0
Thor: Neon Orange	0	0	0.02	0	0	0.03	0.06	0.03	0	0

Figure 12 (above), Table 1. Rate of total occurrences per hour of study of aggressions, human and food interaction behaviors, and play behaviors of the Detroit Zoo gentoo penguins.

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Appendix A

Name	Sex	Species
Thor: Neon Orange	Male	*Pygoscelis papua ellsworthi*
13607: Purple	Female	*Pygoscelis papua ellsworthi*
13606: White	Female	*Pygoscelis papua ellsworthi*
13605: Blue	Female	*Pygoscelis papua ellsworthi*
13604: Yellow	Female	*Pygoscelis papua ellsworthi*
13597: Green	Male	*Pygoscelis papua ellsworthi*
13596: Red	Male	*Pygoscelis papua ellsworthi*
Popeye: Light Blue	Male	*Pygoscelis papua papua*
Philly: Neon Yellow	Female	*Pygoscelis papua papua*
Simon: Pink	Male	*Pygoscelis papua papua*

Appendix A. The gentoo penguins observed. Three (Popeye, Philly, and Simon) are *Pygoscelis paupa paupa* penguins, and the rest of the penguins are *Pygoscelis paupa ellsworthi*. The penguin names are their number or nickname and arm band identifier color.

Appendix B. Ethogram.

All-Occurrence Behavior	**Operational Definition**
Play chase	Individual is part of a pair; erratically swimming, with fast speed (less than 7 seconds across the main pool window) changing direction, orientation, and porpoising in proximity of less than 2 feet (0.6 meters) with one in the lead, then switch direction for bouts lasting longer than 5 seconds.
Play swim	One individual shows repetition of erratic fast swimming (less than 7 seconds across the main pool window), changing direction, and porpoising for bouts lasting longer than 5 seconds.
Mimic	A behavior (indicate behavior) of one penguin is duplicated by another penguin within 10 seconds of the first occurrence
Initiate Mimic	Individual initiates behavior that another penguin mimics
Human Interaction	Staring at human through glass for more than 3 seconds; following human movement or an object a human is holding through glass
Fast synchronized swimming and porpoising	Groups of more than 2 individuals swimming laps at less than 30 seconds per lap, with jumping out of water at least two times in a row across the main pool window
Food Interaction	Biting fish or swimming with fish in beak without eating. May also swim around fish, biting to lift, then sink again
Kleptoparasite	Focal steals food from another individual that has already started eating it (food was in beak)
Receive Kleptoparasitism	Another penguin steals focal's food (food was in focal's beak)
Contact Aggression	Pecking or wing blow directed towards another penguin (indicate species)
Receive Contact Aggression	Pecking or wing blow directed towards a focal penguin (indicate species)
Noncontact Aggression	Lunging or diving at another penguin without making contact (indicate species)
Receive Noncontact Aggression	Another penguin lunging or diving at focal without making contact (indicate species)
Keeper Directed	Focal interacts with keeper; follows or directs behavior to keeper

Proximity	Focal is within one foot (0.3 meter) of another penguin (indicate species)

Scan Behavior

Mimic	Individual was mimicking a behavior at time of scan (indicate behavior in all-occurrence)

Lead Synchronized swimming	Swimming at same pace and direction with two or more individuals, less than 2 meters apart, with focal in lead. Includes changes of direction.
Follow synchronized swimming	Swimming at same pace and direction with two or more individuals, with focal following another penguin. Includes changes of direction.
Repetitive Swim	Swimming across the same space of less than two meters repeatedly with changes in direction to remain in the space, for more than two changes in direction
Surface Swim	Focal is in the water at a depth less than 1 meter from the surface of the pool
Mid-Depth Swim	Focal is in the water at a depth more than 1 meter, but above the bottom of the pool at least 1 meter
Bottom Swim	Focal is in the water at a depth less than 1 meter from the bottom of the pool
Surface Break	Focal keeps head above surface for more than 5 seconds
Porpoise	Leaping in and out of water at least twice in succession
Feeding	Food is more than halfway in mouth, or drinking water
Investigate	Using bill to manipulate objects
Bathing	shaking movement in water; sliding wings over body, tail wagging, and sideways swimming
Contact Aggression	Pecking or wing blow to another penguin- Indicate species in All-Occurrence
Noncontact Aggression	Lunging or diving at another penguin without making contact- Indicate species in All-Occurrence
Not Visible	Focal is not visible to observer at time of scan

Area

South America Tunnel	Focal penguin is in the area of the South America tunnel (first tunnel in sequence of visitors with plain rock walls). Individual can be seen emerging from underwater tunnel, up to edge of submerged land, and under sub-floor tunnel.
Main Pool	Focal penguin is in area under submerged land to edge of main pool window
Antarctica Tunnel	Focal penguin is in the area of the Antarctica Tunnel (second tunnel in sequence of visitors with white walls). Individual is in area from edge of tunnel window to underwater tunnel.
Food Presence	Indicate when there is a presence of fish in the water
Keeper Presence	Indicate when a human is present in the water

Appendix C

Paris Zoo Comparisoin

Methods

At the Paris Zoo in France, the Humboldt penguins are housed in an outdoor habitat with a pool enclosed by glass, about 2 meters deep (Figure 2). There were 17 penguins, and their ages and sex are unknown. These penguins were also identified by arm bands and were observed for two days in July 2017 using the same sampling methods, ZooMonitor Program, and ethogram as the study at the Detroit Zoo (Appendix B). The penguins were only observed when in the water and behavior, location, proximity to other penguins, and food and keeper presence were recorded for each scan. Data was collected over two days, with about 6 hours of total observation (both visible and not visible behaviors to the observer). For both days, the weather was cloudy with intermittent rain showers.

Results

The total percent of visible activity of the Humboldt penguins is summarized in Figure 11A. The top behaviors observed were surface break, surface swimming, synchronized swimming, and bathing. The Humboldt penguins also exhibited a variety of behaviors and were observed to perform many of the same behaviors in the water as the Detroit gentoos (Fig. 13).

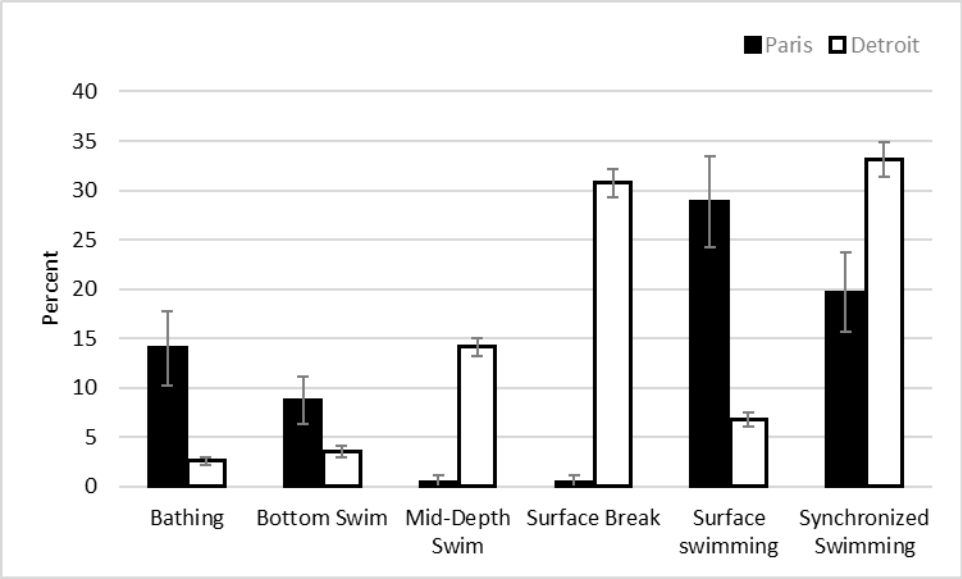

Figure 13. Comparison of average percent of behavior between Humboldt penguins at the Paris Zoo, and gentoo penguins at the Detroit Zoo. A comparison of the top 6 behaviors, which make up more than 70% of behaviors in the Paris and Detroit penguin populations, was made. There was not a significant difference between groups in the percent synchronous swimming, but there were differences in the rest of the behaviors. The Paris Humboldt penguins spent significantly more time bathing ($F_{1,420)} = 30.9$, $P < 0.001$, Fig. 13), bottom swimming ($F_{1,420)} = 7.32$, $P < 0.05$; Fig. 13), and surface swimming ($F_{1,420)} = 53.7$, $P < 0.001$; Fig. 13). The Detroit gentoos spent significantly more time swimming at mid-depth ($F_{1,420)} = 19.2$, $P < 0.001$; Fig. 13), and surface break swimming ($F_{1,420)} = 47.5$, $P < 0.001$; Fig. 13). The differences in behaviors found between the Humboldt and gentoo penguins were expected due to species and habitat differences. The Humboldt penguins live outdoors in a mild climate, while the gentoo penguins live in the Penguin Center. Different species also have different typical behaviors and behavior patterns.