Annotated Bibliography Summaries

**Reference: Tremblay, Y., Y. Cherel. (1999). Synchronous underwater foraging behavior in penguins. Condor 101(1), 179-185.** [**https://doi.org/10.2307/1370462**](https://doi.org/10.2307/1370462)

Summary: The article examined the swimming behaviours of North rockhopper Penguins *Eudyptes chrysocome moseleyi*. Many marine animals typically have consistent foraging and swimming patterns to and from their hunting/foraging grounds. Penguins, in theory, should be no different from any other animals. Trembly and Cherel (1999) used electronic time-depth recorders to examine the foraging patterns seen in *Eudyptes chrysocome mesleyi* penguins. The objective of the study was to observe if these penguins exhibited synchronous foraging behaviours both on the surface and underwater (Tremblay and Cherel 1999). Each penguin was fitted with recorders to observe the depth traveled within a two-day interval, as well as time spent underwater. 25 time-depth recorders were used to track 3-5 birds within the two-day interval. Within the records, only 2 birds were shown to have exact same synchronous diving behaviour. The results showed that these birds (Birds A and B) showed repeated dives at 311 and 309 dives (respectively; although there was a descreptancy of two dives, they were proven to be test dives and not fully committed dives). A comparison of two time/depth graphs were used to examine Birds A and B; different phases were tracked within the 2-day interval. The phase with the highest synchronicity was examined in deeper dives compared to more shallow dives (Tremblay and Cherel 1999). Tremblay and Cherel (1999) provided results that showed that penguins are more likely to accompany each other in deeper dives (as well as evening dives) and towards the same food patch since penguins would benefit more by foraging in pairs towards these patches. Penguins may also dive in pairs to decrease predator threat, as well as allow for alertness for any sort of risk that may come towards their way. The article shows how group foraging and diving synchronicity plays a role in maximizing food uptake.

Contribution: The article provides insight on how penguin diving synchronicity plays a role in foraging behaviour in penguins. The article advances knowledge on paired swimming and diving expeditions can often allow for a potential greater foraging return, and provides more expertise on the group behaviours penguins may show with each other (since penguins are highly colonial). Further studies can be shown on the factor in which penguins choose a partner to synchronously swim with during foraging trips.

**Reference: Green, J. A., Boyd, I. L., Woakes, A. J., Warren, N. L., Butler, P. J. (2005). Behavioural flexibility during year-round foraging in macaroni penguins. Marine Ecology Progress Series 296, 183-196.** [**https://doi.org/10.3354/meps296183**](https://doi.org/10.3354/meps296183)

Summary: The article examined the migration behaviours of *Eudyptes chrysolophus* penguins and its foraging patterns. The objectives of the paper were to understand if penguins modify their foraging behaviour depending on different environmental conditions throughout the year, as well as if the annual cycles show differentiation in “predation pressure” within the foraging area (Green et al., 2005). Green et al., (2005) used data loggers (DLs) on Macaroni penguins within the British Antartic Survey base in Antarctica. The data loggers were used to track dive distance, maximum depth, bottom time duration, and dive duration (Green et al., 2005). The information was collected throughout different phases (incubation, brood, creche, pre-moult, foraging during failed breeding season, and winter phases [early, mid, and late winter]). General linear models as well as the Tukey’s test were used on all variables of the diving periods throughout all 6 phases throughout the year. As a result, they saw a significant variation between penguins in all diving observations; diving duration was significantly higher in the winter compared to surface duration during the winter. However, penguins spent less time underwater during the winter (higher underwater duration during foraging time consequently) (Green et al., 2005). As a result, a dive duration was seen in negative relation to increasing length of day, and vice versa for surface duration. The significance of these findings shows that annual periods throughout all phases of the year may influence prey type and hunting location; the results show consistency in comparison between each season, but not within the season itself (length of day and diving duration is most notably different between summer and winter). A concluding reasoning from the paper is that penguins will change their foraging behaviour in regards to seasonal variations. Further studies can be done on how invading species may alter foraging behaviours on top of seasonal variations.

Contribution: The article provides insight on how the annual patterns of foraging behaviour can be observed and examined in penguins. The article advances greater knowledge and application on tracking penguins year round, and its methodology as well as statistical analysis procedure can be replicated on other animals (especially diving seabirds). Further studies on how annual cycles can be effected by external factors can be looked upon.

**Reference: Ponganis, P. J., Van Dam, R. P., Marshall, G., Knower, T., Levenson, D. H. (2000). Sub-ice foraging behavior of emperor penguins. Journal of Experimental Biology 203(23), 3275-3278.** [**https://doi.org/10.1242/jeb.203.21.3275**](https://doi.org/10.1242/jeb.203.21.3275)

Summary: The article examined the foraging behaviours of *Aptenodytes forsteri* Emperor penguins in shallow dives. Before this paper, much of the observed foraging behaviour was not observable besides heart rate, as well as mass increase before and after foraging trips (Ponganis et al., 2000). The biggest drawback to previous methods was the inability to access a device to record these observations. As a result, the objectives of this paper were to successfully equip recording devices to penguins without effecting foraging behaviours in shallow depths (Ponganis et al., 2000). Ponganis et al. (2000) used Crittercam video cameras to observe *Aptenodytes forsteri* penguins within the sea of McMurdo Sound, Antarctica. The penguins were first trained to wear camera harnesses with the Crittercam camera in order to insure penguins did not negatively react to camera usage. Observation of dives (frequency and duration) were observed in penguins with and without cameras. Results from the diving frequency showed that penguins with cameras only showed dive durations around 20% shorter than without cameras; this proved to show that the cameras were not significant enough to affect foraging behaviour as mass of birds remained relatively consistent. As a result, observations of foraging behaviours were obtained, and through camera imaging, provided the significance of shallow water dives through krill predation.

Contribution: The article provides insight on how advancements in capturing devices can help further confirm previous studies and hypothesis on animal behaviours; in this specific case, the *Aptenodytes forsteri* penguins. The article shows the application of video photography can be further applied on future studies in penguin diving behaviour in regards to different variables and factors.

**Reference: Ainley, D. G., Ballard, G. (2012). Non-consumptive factors affecting foraging patterns in Antarctic penguins: a review and synthesis. Polar Biology 35(1), 1-13.** [**https://doi.org/10.1007/s00300-011-1042-x**](https://doi.org/10.1007/s00300-011-1042-x)

Summary: The article review research looks into the non-consumptive effects of foraging patterns in *Pygoscelis adeliae* Adelie penguins and *Aptenodytes fosteri* emperor penguins. Penguins, like a majority of animals, must gather resources in order to meet energy demands. However, foraging activity can be affected by many factors including abundance of food and predation risk. Antarctic penguins must be able to obtain resources without being preyed upon from predators that forage within the same area. Penguins must exhibit “risk adverse behaviours” by choosing the most optimal time/place to undergo foraging activites (Ainley et al., 2012). Penguins would naturally display behaviours that exist to minimize visual contact towards predators (time spent under water is entirely for transport or foraging, ice crossing whenever available, swimming away from predators…etc). However, the biggest question posed from the article was whether daylight, illumination, or time of day affected penguin foraging behaviour. A prediction the author made was whether or not total darkness effected time spent underwater. Ainley et al (2012) reviewed evidence and as such, produced rational that penguins are able to function in visibly dark waters. However, depending on the time of day and the apparent visibility seen from the surface, penguins will use this discretion toward their foraging behaviour. As a result, the paper hypothesizes that penguins will base their foraging behaviour entirely on amount of surface light visible within water depths, and will tend to avoid night dive foraging to reduce predation risk.

Contribution: This review article shows the importance of external factors not related to energy demands on the foraging behaviour on Antarctic penguins. Time of day influences penguins in their decisions making, as well as their consistent behaviour of risk aversion. As a result, the review shows how penguins have adapted to predation risks through instinctual and visual observations; this can provide an introductory topic on how penguins make rational decisions based on pre-existing behaviours.

**Reference: Mattern, T., Ellenberg, U., Houston, D. M., Davis, L. S. (2007). Consistent foraging routes and benthic foraging behaviour in yellow-eyed penguins. Marine Ecology Progress Series 343, 295-306.** [**https://doi.org/10.3354/meps06954**](https://doi.org/10.3354/meps06954)

Summary: The article examined the foraging behaviours of *Megadyptes antipodes* yellow-eyed penguins, and how it is influenced by consistent foraging routes. Animals from many different species may have consistent patterns when undergoing foraging activities. Whether it’s the actions they may show, or the diet they may uptake, there is a predictable routine that all animals display. Penguins, in theory, should have some sort of predictable mechanism in foraging behaviour. The objective of this paper is to observe if yellow-eyed penguins display consistency of foraging within the same area, as well as the depths in which penguins foraged at. Mattern et al (2007) tracked yellow-eyed penguins through the usage of GPS loggars, as well as time-depth recorders. Both of these devices were on colonies of penguins in order to track distance of foraging, dive duration, and time spent foraging. The data from these were extrapolated and referenced alongside the GPS imaging and tracking of each individual penguins. The results showed that the travelling stage and activity period remained consistent among all penguin individuals, and was verified using ANOVA testing. All penguins within the study exhibited foraging depths that were relative within the benthic region (Mattern et al., 2007). The significance of these findings show that these species of penguins will exhibit consistent foraging within a localized habitat (assuming penguins were not suddenly affected by external factors). The behaviour of consistent foraging could be concluded as an ultimate factor for yellow-eyed penguins, as their consistent foraging routes as well as being well adapted to being bottom feeders are deemed to be highly specialized; this higher degree of specialization is developed through a stabile and predictive environment that allowed penguins to optimize their behaviour for efficient resource uptake (Mattern et al., 2007).

Contribution: The article provides insight on how consistent foraging routes can be observed in foraging behaviours within yellow-eyed penguins. The article provides an in-depth procedural analyses on the movement behaviours of penguins. In doing so, the article provides greater knowledge of how consistent foraging routes is often specialized in an environment that is stabile and predictable. Further studies on foraging routes can be replicated on other species using the same tracking devices – a greater extension on these routes can predict how conflicts may arise within different species through impeding foraging routes.

**Reference: Miller, A. K., Kappes, M. A., Trivelpiece, S. G., Trivelpiece, W. Z. (2010). Foraging-niche separation of breeding gentoo and chinstrap penguins, South Shetland Islands, Antartica. Condor, 112(4), 683-695.** [**https://doi.org/10.1525/cond.2010.090221**](https://doi.org/10.1525/cond.2010.090221)

Summary: The article examined the foraging-niche shown within two co-existing penguin species, *Pygoscelis papua* and *Pygoscelis antarctica* (Gentoo and Chinstrap penguins, respectively). Foraging niches are often developed over years of adaptations and takes into consideration of many different factors such as competition, food abundance, and predation. The objectives of this paper was to find the characteristics of the Gentoo and Chinstrap penguins and their adaptations living amongst each other in the goal of developing a foraging-niche (Miller et al., 2010). The Gentoo and Chinstrap penguins had their mass constantly measured (20 to 40 mass samples were taken throughout the year). Each individual penguins had their location tracked using satellite telemetry, and was tracked throughout the summer and winter seasons. The mass of meal digested, as well as percent of time away from shore and within foraging areas were observed and compared using the ANOVA model. Each variable was co-examined alongside offspring mass and were analyzed using linear regression. The results of this tests show that Gentoo penguins and Chinstrap penguins shared relatively similar preferences for prey within the same testing sites. However, the most notable differences among the two species were the diet composition, time of day of foraging, as well as the distance in which the two species foraged at. Depending on the site of foraging, penguins would favour one type of prey (krill or fish) over the other depending on resource abundance and competition amongst other species. The biggest notable takeaway was that penguins within the same species would exhibit different foraging patterns in different foraging sites, despite being from the same species group (Mattern et al., 2010). The significance of these findings show that site-specific foraging niches play a big role in how penguins exhibit foraging activities and is often developed by the environment around them.

Contribution: The article provides insight on how foraging niches play a huge role in foraging behaviour, and how penguins may revolve their whole foraging patterns based on location of prey, as well as the variability within an environment. The article provides greater knowledge on how foraging niches are one of the most important factors on how penguins may be able to form adaptable behaviours to exist amongst other animals, specifically competition from other penguin species. Further studies on how high variability and external pressures may affect an already developed foraging niche could be done to see how deep foraging niches are ingrained within penguin colonies.

**Reference: Angelier, F., Bost, C. A., Giraudeau, M., Bouteloup, G. (2008). Corticosterone and foraging behavior in a diving seabird: The adelie penguin, Pygoscelis adeliae. General and Comparative Endocrinology 156(1), 134-144.** [**https://doi.org/10.1016/j.ygcen.2007.12.001**](https://doi.org/10.1016/j.ygcen.2007.12.001)

Summary: The article review research looks into the effects of corticosterone on Adelie penguin foraging behaviour. In general, animals will extract resources that will determine the amount of energy exertion on energy taxing behaviours, and as a result, will increase certain energetic demands depending on the situation (such as reproductive activity). Diving seabirds such as the Adelie penguins can combat these difficulties by either increasing the prey quality captured, or by timing reproductive activities during high-foraging activities. Hormonal responses typically are the driving factor to environmental (extrinsic) or intrinsic circumstances. The article reviews research specifically on corticosterone and the effects of elevated corticosterone in pre-foraging birds. Pre-trip and post-trip birds do not experience any sort of physical alterations within the differing corticosterone levels, and body conditions were not affected by elevated corticosterone levels.

 Corticosterone is, however, highly correlated to foraging behaviours. Diving seabirds exhibit either short or long trips during their foraging time; short trips are typically located close to colony range, whereas longer trips expanded far past colony ranges. Penguins were hypothesized to alternate short and long foraging trips for chick feeding and body energy reserves, respectively. Elevated corticosterone birds, however, exhibit lower foraging time underwater compared to the non-elevated corticosterone birds.

 Diving seabirds also show large correlation between parental care and corticosterone secretion. Elevated corticosterone birds were linked with shorter trips with increased foraging effort; higher energy demands due to more energy taxing behaviours exceed coping mechanisms for these demands. Therefore, greater corticosterone secretion is needed, and parental investment is decreased during this period. Ultimately, the paper hypothesizes that corticosterone is an important simulant for increased energetic demand in return for reduced parental care.

Contribution: This review article shows the importance of corticosterone on the foraging behaviour of diving seabird Adelie penguins. Corticosterone is shown to be a key indicator between the balance between foraging effort and reproductive activities. Corticosterone is highly dependent on required energy expenditure during a penguin’s foraging trip. Overall, the review shows many resources in regards to how corticosterone is relevant to many aspects of foraging behaviour, and provides an introductory methodology in which further studies can be looked upon.

**References: Cottin, M., Kato, A. Thierry, A. M., Le Maho, Y., Raclot, T., Ropert-Coudert, Y. (2011). Does corticosterone affect diving behaviour of male adelie penguins? A preliminary experimental study. Ornithological Science 10(1), 3-11.** [**https://doi.org/10.2326/osj.10.3**](https://doi.org/10.2326/osj.10.3)

Summary: The article examined the steroid corticosterone and its role in *Pygosclis adeliae* Adelie penguins. There are many physiological mechanisms that are effectively controlled by endocrine hormones. One of the most effective group of hormones is the glucocorticoids, specifically corticosterone (Cottin et al., 2011). The objectives of this paper were to understand if energy expenditure within foraging trips is affected by an uptake of corticosterone, especially during the breeding season. 4 individual male penguins were chosen, with two of them having implanted corticosterone pellets. Time-depth loggers were used to track duration of dives, number of dives, number of trips, as well as maximum depth of dives. Total amount of dives were observed per trip, as well as longer periods of no diving sessions were observed in birds with corticosterone administration. However, corticosterone administration also increased dive duration at the bottom phase of the dives, while also decreasing the amount of undulations underwater. In regards to the Generalized Estimating Equation (GEE) analysis, the significance of these findings showed that corticosterone induced decreased diving effort, and less distance travelled during foraging trips (Cottin et al., 2011). This finding also correlated with the increased chick mortality rate; the increase in chick mortality during breeding and guarding season is attributed to the redirection of energy allocation from “parental activities to maintenance activities” (Cottin et al., 2011). The significance of these findings shows that corticosterone administration above baseline corticosterone levels reduced foraging effort (less undulations means lack of prey capture), therefore reducing the efficiency during diving trips. The article reaches out that although corticosterone itself is a determining factor of foraging effort, too much of it shows and inverse relationship to higher foraging efficiency.

Contribution: The article provides insight on how glucocorticoids such as corticosterone plays a role in foraging behaviours in penguins. The authors acknowledge previous studies on corticosterone administration (corticosterone measurements), and provide a counter argument in corticosterone causing and inverse relation to foraging effort. This article also provides insight on how corticosterone causes increased chick mortality; further studies on how optimal the effective corticosterone level can be achieved to balance foraging effort with reproductive effort could be explored.

**Reference: Crossin, G. T., Trathan, P. N., Phillips, R. A., Gorman, K. B., Dawson, A., Sakamoto, K. Q., Williams, T. D. (2012). Corticosterone predicts foraging behavior and parental care in macaroni penguins. American Naturalist 180(1), E31-E41.** [**https://doi.org/10.1086/666001**](https://doi.org/10.1086/666001)

Summary: The article examined the steroid corticosterone and its role in the *Eudyptes chrysolophus* Macaroni penguins. Corticosterone is a hormone that is considered as the determining mediator for homeostasis, as well as the mediator for physiological stress in many species. A hypothesis surrounding corticosterone, known as the corticosterone-adaptation hypothesis, states that an upregulation of corticosterone is produced when metabolic demand increase, creating increased fitness within the individual (Crossin et al., 2012). Prolactin, a hormone produced during and after the reproductive stage, was hypothesized to be increased during corticosterone administration (Crossin et al., 2012). The objectives of this paper were to find if the increase in corticosterone levels caused an increase in time spent at sea, an increase of body mass (in both parents and chicks), (Crossin et al., 2012). Cross et al. (2012) used coloured water paint on both females and males with offspring (during brood-guard stage). Blood samples were taken from marked females, and time-depth recorders were planted on all marked penguins (total of 17 female locations). Female variable penguins were implanted with a subcutaneous tag with a corticosterone implant, and chick mass (offspring from marked females) were measured before and after implantation. Distance, depth, and duration of dives were all measured through the time-depth loggers, and were run through a MANCOVA model and multiple ANOA tests (multivariate and univariate tests). All tests show a significant increase in mass gain that correlated to the increased number of dives in corticosterone administered penguins (ANOVA showed a significant p-value in mass pre and post corticosterone alteration). An increase in diving number and duration was also seen in corticosterone implant subjects. However, there was no difference in prolactin secretion; prolactin was not a direct factor in foraging behaviour in macaroni penguins (Crossin et al., 2012). The significance of the findings show that corticosterone increases foraging effort post-administration, but does not affect prolactin production (regardless if parental activity increased).

Contribution: The article provides insight on corticosterone plays a role in both foraging and parental behaviours in penguins. The article tries to find a linkage between the hormone corticosterone and prolactin, and if an increase in corticosterone uptake would cause positive feedback towards the secretion of another hormone. Ultimately, the article disproves this linkage, but provides greater knowledge in the corticosterone-adaptation hypothesis. Further studies can be done on corticosterone on penguins in terms of external factors and physiological stress; how can upregulation of corticosterone help with the adaptation process of penguins?

Reference: Cottin, M., MacIntosh, A. J. J., Kato, A., Takahashi, A., Debin, M., Raclot, T., Ropert-Coudert, Y. (2014). Corticosterone administration leads to a transient alteration of foraging behaviour and complexity in a diving seabird. *Marine Ecology Progress Series 496*, 249-262. <https://doi.org/10.3354/meps10618>

Summary: The article examined the steroid hormone corticosterone and its role in the diving seabird Adelie penguin. Corticosterone is a hormone that regulates metabolic processes in most living animals, leading to studies on the effects of energy dispersion during foraging. The objectives of the paper were to understand if foraging behaviours of diving seabirds, complexity of diving periodicity, and parental behaviours changed post corticosterone level alteration. Cottin et al. (2014) used distance loggers and trackers to show how increased corticosteroid uptake plays a role in trip duration (time per foraging trip), number of dives, duration of dives (time it takes to complete a dive), and maximum distance of dives. Blood samples were taken from all individual penguins (20 male penguins) and 2 pairs of chicks per adult male. Of the 20 male penguins, half were tagged with corticosterone pellets, and half were the control group. Subjects with increased corticosterone exhibited decreased duration of trips, as well as decreased time spent underwater, increased maximum diving depth, and showed significant difference from the control group using both a linear regression model and ANOVA model (increased complexion of diving periodicity). Cottin et al. (2014) provided context in which the penguins increased diving efficiency (time spent underwater) by increasing prey-capture rate (either an increase in prey capture or quality of prey). The significance of these findings show that corticosterone is a driving factor in foraging activities by maximizing trip efficiency without any physical drawbacks (mass of the experimental group and control group) The results also showed that corticosterone displayed no significant difference in terms of parental behaviour (feeding behaviour towards offspring were not significantly different between experimental and control groups). The article reaches out how further studies can be done on how foraging behaviour complexity and foraging success is related to each other with the alteration of corticosterone.

Contribution: The article provides insight on how hormones such as corticosterone can influence large foraging behaviours in penguins. The article advances knowledge in how corticosterone can be mediated to increase foraging efficiency in penguins. In doing so, the article provides greater knowledge of corticosterone and its role of energy dispersion and diving efficiency during foraging trips; this provides more information on further implementation of corticosterone beyond its role in maintaining metabolic processes. Further studies on corticosterone on penguin prey-success rate and its neurological mechanisms can be done to explain how greater efficiency is achieved post-corticosterone alteration.