Variation in Emperor Goose (*Anser canagicus*) Body Mass at the Geographic Extremes of their Wintering Range

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Abstract

The emperor goose (*Anser canagicus*) is a waterfowl species that is endemic to the Bering Sea and holds great ecological, recreational, and cultural value. Emperor geese are unique in their wintering behaviors as they migrate only slightly south of their summer breeding grounds in the Yukon-Kuskokwim Delta to non-breeding wintering grounds that are at relatively high latitudes along the Aleutian Islands, Alaska Peninsula, and the Kodiak Archipelago. Recent declines in emperor goose populations brings to light the importance of developing a more comprehensive understanding of emperor goose ecology, with a particular focus on understanding previously understudied aspects of their wintering ecology. This study explores differences of body mass as a proxy for individual fitness between two wintering sites that represent the geographic extremes of the emperor goose wintering distribution: Shemya Island and the Kodiak Archipelago. A significant difference in body mass between Kodiak and Shemya was observed amongst all adult geese, specifically amongst female adults, with geese on Shemya having lower body mass than the geese on Kodiak in these demographic groups. Additionally, it was observed that variation in body mass among emperor geese could be explained by additive effects of age class, sex, and field site. These findings indicate that differences in environmental conditions, food source availability, and migration distance to the different wintering sites between Shemya and Kodiak could explain why some demographic groups of emperor geese displayed significantly lower body masses, and therefore lower fitness, at Shemya (i.e. longer winter migration, extreme environment, lower access to protein-rich food). Understanding the wintering ecology of emperor geese and dedicating more time and resources to explaining variability in fitness experienced by emperor geese at their wintering sites is critical for understanding how to best move forward with conservation and management strategies that prevent further population declines.

Introduction

Migration to suitable wintering grounds is a vital strategy that many migratory species use to enhance survival during the non-breeding season (Salewski and Bruderer 2007). For many species, wintering sites with adequate conditions and abundant resources are crucial for an individual's survival and reproductive success (Guillemain et al. 2010). However, for some migratory species, it can be particularly difficult to gather data during migration or while at wintering sites due to increased movement and less concentrated populations; as a result, the majority of studies about the physiological and behavioral conditions of migratory species is conducted while populations are relatively sedentary and have restricted movement at their summer breeding grounds (Schultner et al. 2014). Despite the lack of information about the wintering sites of migratory species, the time that a species spends at its wintering sites is an extremely important component of their life cycle that should not be overlooked (Bairlein 2003). In order to properly and effectively conserve migratory species, a complete understanding of wintering sites is crucial to understand how to best allocate resources and efforts towards migratory bird species conservation.

The environmental context at wintering sites can be particularly important for migratory waterfowl species in determining the fitness and overall condition of individual birds. As seen in Mallards (*Anas platyrhynchos*) and Teals (*Anas crecca*), body mass has increased significantly over the past 30 years (11.7%) as conditions at wintering sites have become more mild due to a warming climate (Guillemain et al. 2010). Additionally, a variety of waterfowl species have been observed to visit wintering sites where there are more nutrient-dense food sources and warmer, milder wintering site temperatures (Roberts et al. 2016). Because the combination of highly caloric resources and milder winter conditions helps reduce lipid-loss, birds are heavier and better able to successfully survive migration at wintering sites with these environmental and nutritional conditions (Roberts et al. 2016). Not only do the conditions once a species arrives at a wintering site impact the survival, fitness, and body condition of migratory birds, but the migrational journey to these wintering sites may also contribute to the physiological stress endured by migratory species (Vágási et al. 2016; Roberts et al. 2016). Longer migration routes to these given wintering sites can result in significant increases in physiological stress and fitness costs, potentially having negative effects on body condition of migrants that partake in longer migrations (Vágási et al. 2016). In summary, various previous studies suggest that wintering sites that have more benign winter conditions (e.g. warmer temperatures, less intense storms), more readily accessible resources (e.g., food), and less physiologically stressful environmental conditions (e.g. shorter migration distance, minimal ice or snow cover) support greater body mass, fitness benefits, and increased survival in avian migratory species (Guillemain et al. 2010; Roberts et al. 2016; Vágási et al. 2016; Lake et al. 2008; Wang et al. 2013).

Emperor geese (*Anser canagicus*) (Fig. 1) is a species of migratory waterfowl that is endemic to the Bering Sea area (Uher-Koch et al. 2021; Fig. 2). Emperor geese are known to migrate from summer breeding grounds in Western Alaska on the Yukon-Kuskokwim Delta to non-breeding wintering grounds along the Aleutian Islands, Alaska Peninsula, and the Kodiak Archipelago (Uher-Koch et al. 2021; Fig. 2). Their wintering range is characterized by geographic and environmental variability, correlating with significant variability in migration and wintering strategies, and thus variable fitness costs for the geese (Uher-Koch et al. 2021).


Figure 1: Emperor goose after being extracted from rocket net and being handled for data collection. Picture taken by L. Aubry.

Emperor geese are unique compared to other geese species because while they do migrate slightly south of their summer breeding grounds during the winter, their wintering grounds are still at relatively high latitudes (Hupp et al. 2008). Other geese species, such as tule geese (*Anser albifrons elgasi*), tend to summer in Alaska and then migrate to wintering grounds as far south as California, which are at much lower latitudes compared to summering grounds (Ely et al. 2007). Additionally, there is a significant amount of geographic and environmental variation in the wintering grounds of emperor geese (Hupp et al.

2008). While some avian species tend to have a very concentrated range of wintering sites with very little variability, emperor geese have a wintering range that spans more than 3,000 kilometers from Kodiak Island of Alaska to the Commander Islands of Russia and is characterized by geographic, ecological, and environmental heterogeneity (Wang et al. 2013; Hupp et al. 2008). Therefore, the uniqueness of emperor geese and their migration/wintering strategies warrants further exploration and could hold the key to understanding and designing effective management strategies to best conserve emperor geese.

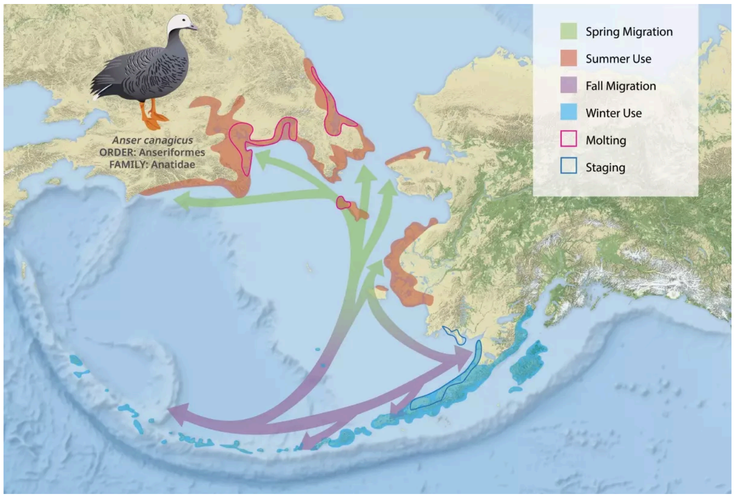


Figure 2: This map details the distribution and migration paths of emperor geese. Produced by U.S. Fish and Wildlife Services, publication date: Jan 18, 2022.

Emperor geese are not only unique ecologically, but they also are an extremely important species for Alaska Indigenous peoples as a species that holds cultural significance and is hunted as a subsistence species to provide food for rural Alaskans and Indigenous peoples, especially during the late spring when other sources of food are scarce (Mengak et al. 2022). Additionally, emperor geese are also a highly sought-after species for recreational hunters and birdwatchers (Mengak et al. 2022). However, after a sharp decline in emperor geese populations over 22 years from over 100,000 individuals in 1964 to less than 45,000 individuals in 1986 due to reasons that are still poorly understood, both recreational hunting and subsistence hunting of emperor geese were closed in 1986 and 1987 respectively (Pacific Flyway Council 2016). These hunting closures remained in place for 30 years while emperor geese populations slowly rebounded (Pacific Flyway Council 2016). Hunting restrictions were lifted in 2017 once emperor geese rose above the minimum population abundance management quota (Pacific Flyway Council 2016). However, quickly after hunting restrictions were lifted, emperor geese populations declined once again (Frost et al. 2024). In order to better understand why emperor geese populations have recently declined, it is crucial to develop a more complete understanding of emperor goose ecology and biology, including investing more resources into understanding the wintering habits and habitats of emperor geese.

Prior work suggests that wintering sites that are farther west along the chain of the Aleutian Islands are more physiologically taxing for emperor geese than wintering sites to the east (Hupp et al. 2008). Emperor geese that winter at sites that are farther from the summer breeding grounds take advantage of staging areas during migration, and stop more often along their migration path, suggesting physiological stress (Hupp et al. 2008). Meanwhile, geese that winter closer to the Alaskan coast and summer breeding grounds are able to fly straight from the Yukon-Kuskokwim Delta to their winter grounds without stopping at staging areas, indicating a less energetically costly and physiologically stressful winter migration (Hupp et al. 2008).

Additionally, Uher-Koch et al. (2021) indicated that the wintering habits of emperor geese may have recently shifted, with wintering sites closer to mainland Alaska, such as Kodiak, supporting larger populations of emperor geese in recent years, as opposed to wintering sites near Russia and the western end of the Aleutian Islands. In addition, birds appear to be in better body condition on Kodiak and other wintering sites closer to mainland Alaska than at wintering sites farther West along the Aleutians (Uher-Koch et al. 2021).

Whilst a number of studies looked at the more broad-scale distribution and migration patterns of emperor geese, relatively few have focused on analyzing the differences in resource availability, diet, body mass, and body condition along their wintering range to evaluate variation in the suitability of different wintering sites. Additionally, most analyses and studies that have focused on physiological and habitat conditions of emperor geese have collected data at their breeding summer grounds with a focus on documenting changes in recruitment, reproduction, and annual survival across summer and breeding seasons, leaving a notable gap in our understanding of wintering conditions (Shmutz 2001; Lewis et al. 2021; Lake et al. 2008). A complete picture of the conservation issues facing emperor geese (including issues facing emperor geese during wintering) is needed to best manage emperor goose populations moving forward.

In an attempt to understand variation in the condition of emperor geese across their wintering grounds, body mass will be used as a proxy for individual fitness and will be compared across two extremes of the wintering range, with data from Kodiak Island representing the eastern-most portion of their wintering range, and data from Shemya Island representing the western-most wintering sites in their wintering range along the Aleutian Islands. Shemya Island is a relatively small, remote island that is known to support a stable, though small, population of emperor geese during the winter season (Uher-Koch et al. 2021; Pohlen 2023). The Kodiak Archipelago is located closer to mainland Alaska and is known to support an increasing population of emperor geese throughout winter months (Wilson 2016; Uher-Koch et al. 2021). The objective of this study is to identify differences in body mass between emperor goose populations that winter on Kodiak Island versus Shemya Island. Based on the energetic constraints of a longer migration, the harsher winter condition, and the relatively lower availability of protein rich foods, I predict the average body mass of emperor geese will be significantly lower on Shemya Island than on Kodiak.

Methods

Study Area

Shemya Island is one of the westernmost islands along the Aleutian Island chain, located approximately 1,500 kilometers west of mainland Alaska (Uher-Koch et al. 2021). Shemya is a relatively small island with a length of only 7 kilometers and a width of approximately 2 kilometers and compared to many other islands along the Aleutian Islands chain, Shemya has very little variation in altitude, maintaining a characteristically flat profile (Gates et al. 1971; Gibson 1981). Shemya is characterized by rocky shores with occasional sandy beaches and small freshwater lakes, wetlands, and streams inland (Uher-Koch et al. 2021). The biotic landscape of Shemya is composed of grasses, sedges, algae, mosses, lichens, and low-laying forbs and shrubs (Uher Koch et al. 2021). The average monthly temperatures found on Shemya Island range from -1 degrees Celsius in January to 10 degrees Celsius in August with annual precipitation exceeding 80 centimeters (Uher-Koch et al. 2021). Shemya is also frequently exposed to powerful and harsh cyclonic storms characterized by strong winds and intense temperature fluctuations that originate in the Bering Sea (Uher-Koch et al. 2021; Gibson 1981).

The other study site from which emperor geese populations were studied and surveyed was Women's Bay, on the Kodiak Archipelago. The Kodiak Archipelago is located in the Gulf of Alaska and is only 32-48 kilometers south of mainland Alaska (Fitzhugh 2003; Vincent 1964). The Kodiak Archipelago is a collection of 14 islands that is approximately 290 kilometers in length with a total area of 12,692 kilometers squared (Vincent 1964). Kodiak is characterized by deep valleys, mountainous ranges, and sharp ridges caused by glacial retreat (Fitzhugh 2003). Kodiak has great variety in altitude, with peaks reaching 1,219 meters and overall greater abiotic/environmental heterogeneity across the archipelago, creating intricate subhabitats (Vincent 1964). The biotic landscape of Kodiak includes more vegetative diversity and structure with *Picea sitchensis* being a prominent species and many woody shrubs along with a variety of grasses and sedges while mosses, lichens, and algal mats are not as prominent on Kodiak as they are on Shemya (Vincent 1964). Additionally, there anecdotally appears to be a great concentration of mollusks and crustaceans easily accessible on Kodiak relative to Shemya (R. Thomas, pers. comm.). The Kodiak Archipelago is unique because it is located along the trajectory of the Alaska Current, which carries warmer water, resulting in the prevention of ice formation along the coasts of the Kodiak Archipelago and dampens intense temperature fluctuations year round (Fitzhugh 2003). The average temperatures typically found on the Kodiak Archipelago include an average minimum temperature of -17 degrees Celsius and average maximum temperature of around 26 degrees Celsius with annual precipitation reaching around 150 to 200 centimeters (Fitzhugh 2003; Vincent 1964). Kodiak also presents milder overwintering conditions due to regional protection in the Gulf of Alaska from large and harsh storm systems and localized protection in the form of sheltered bays like, Women's Bay (Eisenhauer and Kirkpatrick 1977).

Field Methods

At each study area, rocket nets were used to capture emperor geese. Rocket nets were set up at both predetermined and not predetermined sites. Emperor geese are known to frequent freshwater seeps to obtain drinking water and areas where there is a particularly dense concentration of food resources. Therefore, rocket nets were set up in these freshwater seeps or food resource-rich hotspots as emperor geese could reliably be observed at these locations. Rocket nets were also established near observed groups of geese at sites that were not necessarily predetermined and geese were then corralled into the capture zone. Depending on lighting and weather conditions, emperor goose decoys were often placed near the rocket net in an attempt to attract emperor geese and encourage them to land near the rocket net.

Rocket nets ensured that the capture of emperor geese was relatively random and unbiased as individual geese were not targeted or pursued for capture. The rocket netting does not inherently result in any bias towards any one given demographic of emperor geese, allowing for a randomized and representative sampling of emperor geese across a large spectrum of demographic characteristics.

When emperor geese were captured under the rocket net, individual geese were removed from the net and age, sex, total culmen length, total tarsus length, and body mass data were collected for each individual bird. In order to determine the body mass of individual geese, captured geese were placed in a tared weighing bin that held them while their weight was measured on a scale. geese were cloacally sexed upon capture. In order to age geese, the head feathers and the color of the feet of the geese were observed (Fig. 3). Adult geese were identified as individuals that had darker orange legs and a pure white head (Fig. 3). Meanwhile, juvenile geese were identified as individuals that typically had darker/black speckled coloration on head feathers and pale orange legs (Fig. 3).

Figure 3: This image displays a juvenile emperor goose (left) next to adult emperor goose (right). The juvenile has a mottled and speckled head while the adult has a pure white head. Head coloration was used to identify whether captured individuals were adults or juveniles. Picture taken by R. Thomas.

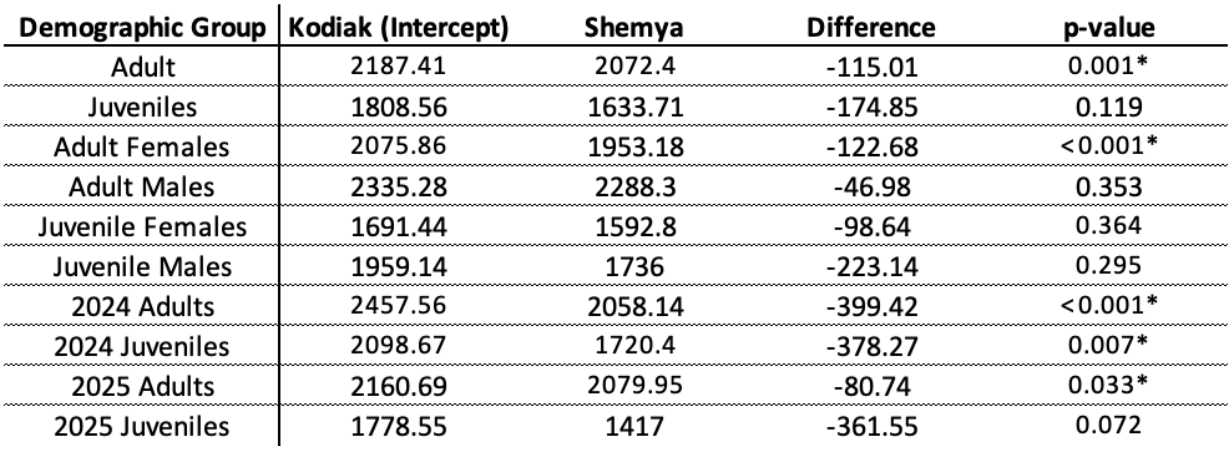
Statistical Methods

Statistical analyses were split up into two separate sets. In the first set, linear models were constructed from data subsetted by sex (females vs. male), age class (adult vs. juvenile) and capture year (2024 vs. 2025). Each model accounted for field sites to be able to observe body mass differences across locations (Shemya vs. Kodiak). Pairsize comparisons were used and p-values less than 0.05 ($p\text{-value} < 0.05$) supported significant differences across groups (e.g. location, year, sex, age).

In the second set, we used a model selection framework to further investigate which effects best explain variability in body mass whilst exploring interactive, additive, and individual effects of sex, field site, and age (Burnham and Anderson 2002). Akaike's Information Criterion model selection framework was used to rank models based on their fit to the data (Akaike 1973). A total of seven linear models were constructed and were compared, including a null model (i.e. no effect modelled on body mass) using an AIC (Akaike 1973). These models include (1) a null model, (2) a model that captured an age effect, (3) an additive effect of age and field site, (4) an interactive effect of age and field site, (5) an interactive effect of age and field site with an additive effect of sex, (6) an interactive effect of sex and field site with an additive effect of age, and (7) additive effects of age, sex, and field site. The model with the smallest AIC value was identified as the most parsimonious model that best explains variation in emperor goose body mass. The models that proceeded to have the smallest AIC value and any additional models that had a Delta AIC value of less than 2 ($\text{Delta AIC} < 2$) were analyzed using a q-q plot to ensure residuals were normality distributed and linear assumptions were met.

Results

Wintering location was a significant predictor of body mass (Table 1) with body mass lower at Shemya than Kodiak for adults (Fig. 4). Indeed, adults captured on Kodiak weighed 2187.41 grams on average, while adults captured on Shemya weighed 2072.4 grams on average, which resulted in a significant difference between study sites (p-value = 0.001) (Table 1). However, we did not detect a difference in body mass among juveniles between Kodiak and Shemya (p-value = 0.119) (Table 1).



Demographic Group	Kodiak (Intercept)	Shemya	Difference	p-value
Adult	2187.41	2072.4	-115.01	0.001*
Juveniles	1808.56	1633.71	-174.85	0.119
Adult Females	2075.86	1953.18	-122.68	<0.001*
Adult Males	2335.28	2288.3	-46.98	0.353
Juvenile Females	1691.44	1592.8	-98.64	0.364
Juvenile Males	1959.14	1736	-223.14	0.295
2024 Adults	2457.56	2058.14	-399.42	<0.001*
2024 Juveniles	2098.67	1720.4	-378.27	0.007*
2025 Adults	2160.69	2079.95	-80.74	0.033*
2025 Juveniles	1778.55	1417	-361.55	0.072

Table 1: This table shows the average body masses of each demographic group on the Kodiak Archipelago and on Shemya Island. The difference between body mass was calculated by subtracting the average body mass of emperor geese in a given demographic group on Kodiak from the average body mass of emperor geese on Shemya, providing a difference between the two masses. The p-value indicated the significance of these differences in body mass between Kodiak and Shemya. p-values that are less than 0.05 ($p<0.05$) were considered significant differences and were therefore, marked with a '*' to indicate significance.

Adult females on Kodiak had an average body mass of 2075.86 grams while the adult females on Shemya Island weighed 1953.18 grams on average, indicating a significant difference between study sites (p-value < 0.001; Fig. 5) (Table 1). We did not, however, detect a significant difference in body mass for adult males across study sites (p-value = 0.353) (Table 1). There was no significant difference in body mass between juvenile females on Shemya versus Kodiak (p-value = 0.364), and the same went for juvenile males (p-value = 0.295) (Table 1).

Figure 4: A boxplot of adult emperor geese body mass captured at two different wintering sites shows adult emperor geese captured on Kodiak have an average body mass that is significantly greater than the average body mass of adult emperor geese captured on Shemya. Data collected from adults on Kodiak are represented in a teal color while data collected from adult females at Shemya Island are represented by a mint green color. The sample size is 100 on Kodiak (N=100) and 104 on Shemya (N=104) for a total of 204 (N=204).

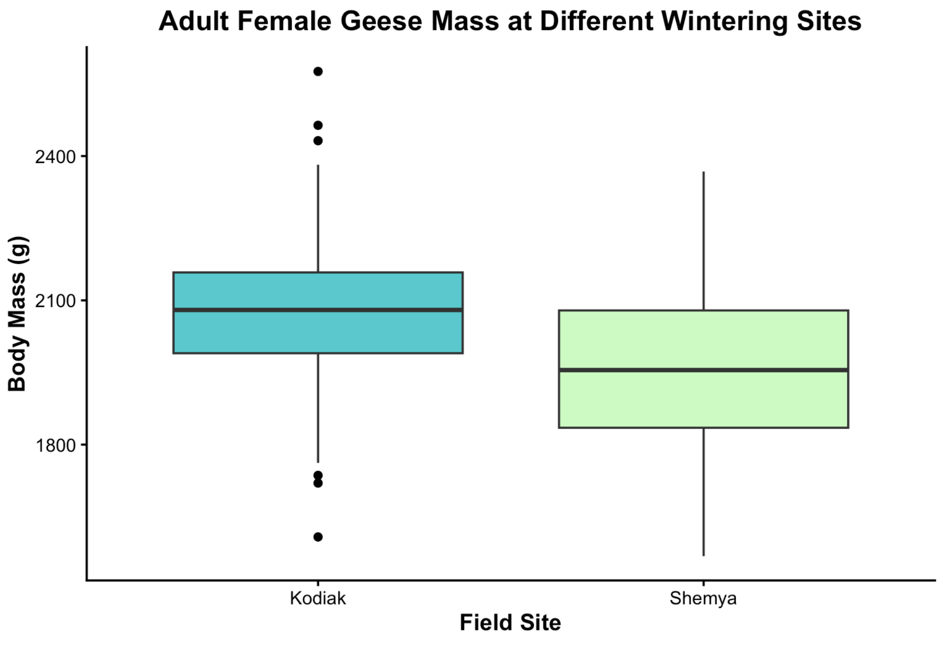
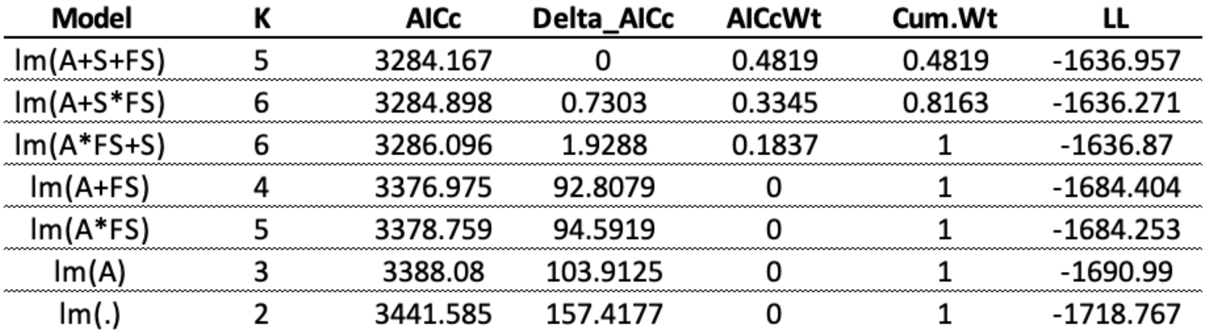


Figure 5: A boxplot of adult female emperor geese body mass captured at two different wintering sites shows adult female emperor geese captured on Kodiak have an average body mass that is significantly greater than the average body mass of adult female emperor geese captured on Shemya. Data collected from adult females on Kodiak are represented in a teal color while data collected from adult females on Shemya are represented by a mint green color. The sample size is 57 on Kodiak (N=57) and 67 on Shemya (N=67) for a total of 124 (N=124).

When subsetting data by age and capture years, we found that adult geese captured in 2024 on Kodiak had an average body mass of 2457.56 grams while the adults captured the same year on Shemya had an average body mass of 2058.14 grams (p-value < 0.001) (Table 1). There was also a significant difference in juvenile body mass between individuals captured at Kodiak versus Shemya in 2024 (p-value = 0.007), where juvenile geese captured on Kodiak were heavier (average body mass of 2098.67 grams) than on Shemya (average body mass of 1720.40 grams) (Table 1). Adults captured on Kodiak Archipelago in 2025 were on average marginally heavier (2160.69 grams) than adults captured on Shemya the same year (2079.95 grams) (p-value = 0.033) (Table 1). However, there was no significant difference among juveniles captured in 2025 between Kodiak and Shemya (p-value = 0.072) (Table 1).

AIC model selection results indicated that the model that was the most parsimonious in explaining variation in body mass established an additive effect of age, sex, and field site (Table 2, AIC weight = 48.19%). The second most parsimonious model included an additive effect of age and sex, and an interactive effect of sex and field site (Table 2, AIC weight = 33.45%; Delta AIC < 2). The third most parsimonious model included an interactive effect of age and field site, and an additive effect of sex (Table 2, AIC weight = 18.37%; Delta AIC < 2). All effects captured in the most parsimonious model (i.e. Age + Sex + Field Site; Table 3) explained significant variability in body mass (Table 3). In the second best performing model (i.e. Age + Sex * Field site; Table 4), all effects were also significant with the exception of the interaction between sex and location (Table 4).



Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
lm(A+S+FS)	5	3284.167	0	0.4819	0.4819	-1636.957
lm(A+S*FS)	6	3284.898	0.7303	0.3345	0.8163	-1636.271
lm(A*FS+S)	6	3286.096	1.9288	0.1837	1	-1636.87
lm(A+FS)	4	3376.975	92.8079	0	1	-1684.404
lm(A*FS)	5	3378.759	94.5919	0	1	-1684.253
lm(A)	3	3388.08	103.9125	0	1	-1690.99
lm(.)	2	3441.585	157.4177	0	1	-1718.767

Table 2: Akaike's Information Criterion model selection framework when analyzing models that attempt to explain variation in body mass of emperor geese. "A" represents "Age" (adult or juvenile), "S" represents "Sex" (male or female), and "FS" represents "Field Site" or wintering site (Shemya or Kodiak). "*" represents an interactive effect and "+" represents an additive effect.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	2064.97	23.21	88.961	< 2e-16 ***
Juvenile	-388.98	37.04	-10.501	< 2e-16 ***
Male	289.23	27.07	10.685	< 2e-16 ***
Shemya	-97.32	27.39	-3.554	0.000457 ***

Table 3: Summary statistics for the most parsimonious model which included an additive effect of Age, Sex, and Field Site (lm(A+S+FS), Table 2). The intercept represents the reference group of adult females captured on Kodiak. The significance codes for this table are as follows: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1, with ‘*’ indicating significant effects (below the 0.05 significance threshold, and ‘ ’ indicating a lack of significance).

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	2076.79	25.33	81.990	< 2e-16 ***
Juvenile	-388.29	37.02	-10.489	< 2e-16 ***
Male	261.47	36.10	7.244	6.04e-12 ***
Shemya	-121.67	34.48	-3.529	0.0005 ***
Male:Shemya	63.29	54.52	1.161	0.2468

Table 4: Summary statistics for the second most parsimonious model and established that Age had an additive effect with Sex and Sex had an interactive effect with Field Site (lm(A+S*FS), Table 2). The intercept represents the reference group of adult females captured at the Kodiak Archipelago. The significance codes for this table are as follows: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1, with ‘*’ indicating significant effects (below the 0.05 significance threshold, and ‘ ’ indicating a lack of significance).

Discussion

We hypothesized that emperor geese that wintered at Kodiak would have a greater body mass than individuals that wintered at Shemya due to higher quality food resources, less harsh environmental conditions, and a shorter migration distance from the breeding grounds. Whilst some demographic groups did not display any significant differences in body mass between Shemya and Kodiak (e.g. juveniles), some did, such as all adults and specifically adult females. Model selection results further suggest that the most parsimonious explanation for variations in body mass was due to an additive effect of age class and an interaction between sex and field site, indicating that to some degree, field site does indeed impact variation in body mass among emperor geese (Table 2).

Adults captured at Kodiak were heavier than adults captured at Shemya in 2024 and 2025, both when data from 2024 and 2025 were considered together and separately (Fig. 4, Table 1). One potential reason why adults at Kodiak were heavier could be milder winter weather at Kodiak (Guillemain et al. 2010; Uher-Koch et al. 2021; Gibson 1981; Eisenhauer and Kirkpatrick 1977). Harsh winter conditions (larger storms, stronger winds, intense temperature fluctuations etc.) result in decreased body condition and can negatively impact survival rates of emperor geese (Uher-Koch et al. 2021). Shemya has a less protected coastline and is characterized by more intense winter storms, potentially resulting in greater energy expenditure in an attempt to survive harsh winter conditions and therefore, decreased body mass can be observed in emperor geese populations on Shemya, indicating decreased fitness and potentially lower survival of Shemya individuals compared to Kodiak (Fig. 4; Schmutz 1993).

Another potential reason adult emperor geese had lower body mass on Shemya could be variation in the quality of food resources available at Shemya. Emperor geese tend to have an omnivorous diet, feeding on a combination of bivalve prey, crustaceans, algae, and a variety of vegetation, including grasses, seaweed, and sedges (Schmutz 1994; Eisenhauer and Kirkpatrick 1977). Emperor geese have been observed to exhibit higher feeding intensities at sites that are rich with mussels and animal prey sources, falling back on more vegetation-dense feeding sites mostly when these animal prey sources were not easily accessible (Schmutz 1994). This suggests emperor goose may favor these areas that are abundant with sources of animal prey due to the nutritional and caloric benefits of animal prey when supporting physiological functions compared to the vegetation, which lacks nutritional and caloric substance (Schmutz 1994). Shemya notably lacks dense populations of the barnacles and mussels that supplement a high fat and protein diet for emperor geese and, as a result, geese on Shemya must resort to a diet that consists of nutritionally-poor vegetation (i.e. based on food item collection, anecdotal fecal sample assessments, and stable isotopic analysis conducted at both wintering sites; R. Thomas et al. in preparation). Meanwhile, dense populations of bivalves and crustaceans on Kodiak indicate emperor geese have access to more nutrient-rich food sources (R. Thomas et al. in preparation).

A final explanation that could explain the significant difference in body mass between adult emperor geese on Shemya versus Kodiak could be the physiological stress associated with the longer migration to Shemya. Longer migrations are known to increase physiological stress, requiring birds to deplete fat stores to a greater degree during these longer migrations, and could explain the significantly smaller body mass of individuals that migrated notably longer distances to reach wintering sites on Shemya (Vágási et al. 2016; Hupp et al. 2008).

A particularly interesting result was the fact that adult females exhibited statistically significant differences in body mass between Shemya and Kodiak (Fig. 5), whilst adult males did not. In general, the survival of adult females is typically lower than adult male survival after the summer breeding season (Schmutz et al. 1994). Likely, the physiological stress that females experience during reproduction results in female geese having depleted endogenous reserves prior to migration due to a disproportionate investment in incubating and rearing offspring (Schmutz et al. 1994; Thompson and Raveling 1987). Such depletion makes females more susceptible and energetically vulnerable to the physiological stressors that come with migration, and particularly with the longer migration to Shemya. Meanwhile, males may have adequate endogenous reserves that they did not expend laying, incubating, and rearing offspring, meaning males are more able to maintain a higher body mass and sufficient fitness during migration, regardless of migration distance, resulting in a significant difference in body mass for adult females between the two wintering sites, but not adult males (Batt et al. 1992).

Many of the models that accounted for age class did not result in statistically significant differences in body mass of juveniles on Shemya versus Kodiak. This may have been due to the relatively small sample size of juveniles in this study, making it difficult to determine any significant differences that may exist in juvenile body mass between the wintering sites. However, juvenile body mass was systematically low at both sites, and much lower than adult body mass, as expected.

The linear model that best fit the data proposed that there is an additive effect of age, sex and field site explaining variation in body mass (Table 2, Table 3, Fig. 6). The magnitude of the effect of age on body mass was the same for both males and females; the effect of sex on body mass was the same for adults and juveniles, and the magnitude of the effect of field site was the same across sex and age classes. This additive model addresses the main factors that may impact body mass, as it is known that males are on average heavier than females, adults are on average heavier than juveniles, and field site for certain demographic groups, can significantly impact the body mass of individuals (Figs. 3 & 4, Table 1). So essentially, like age class and sex, field site is also an important variable in determining the body mass of emperor geese according to this most parsimonious model from the AIC output (Table 2). The other models analyzed in the AIC model selection framework that account for interactive effects may be less parsimonious because while it accounted for all of the variables that may impact body mass (e.g., sex, age, and field site), it introduced excessive complexity (i.e. additional effects and parameters) that the AIC model selection framework penalizes, where the interaction between age class and field site was not significant. This result mostly highlighted that we did not detect a significant difference in body mass across field sites among juveniles, and adult males, yet, we did detect a difference in body mass across sites among all adults (male and female), and female adults in particular.

While body mass can be used as an indicator of the general condition of an individual bird, investigating body mass is not the same as investigating a direct measurement of the body condition in birds (Labocha and Hayes 2012). When only looking at mass, there is a failure to account for differences in structural size among individuals, as mass is not a strict measurement of body fat (Labocha and Hayes 2012). In this particular study, we corrected body mass by accounting for differences in age class, as juveniles are structurally smaller than adults, and therefore, will have a lower body mass. However, in order to have a more accurate interpretation of the fitness and health of emperor geese, one could correct body mass by a structural metric, such as tarsus length, to account for variation in structural size even within the same age class, as even among the age class of adults some individuals can be structurally larger or smaller than others (Labocha and Hayes 2012). Note that we have conducted body condition analyses, and the results were qualitatively in line with the body mass results presented herein. We decided to focus only on body mass results herein for the sake of conciseness.

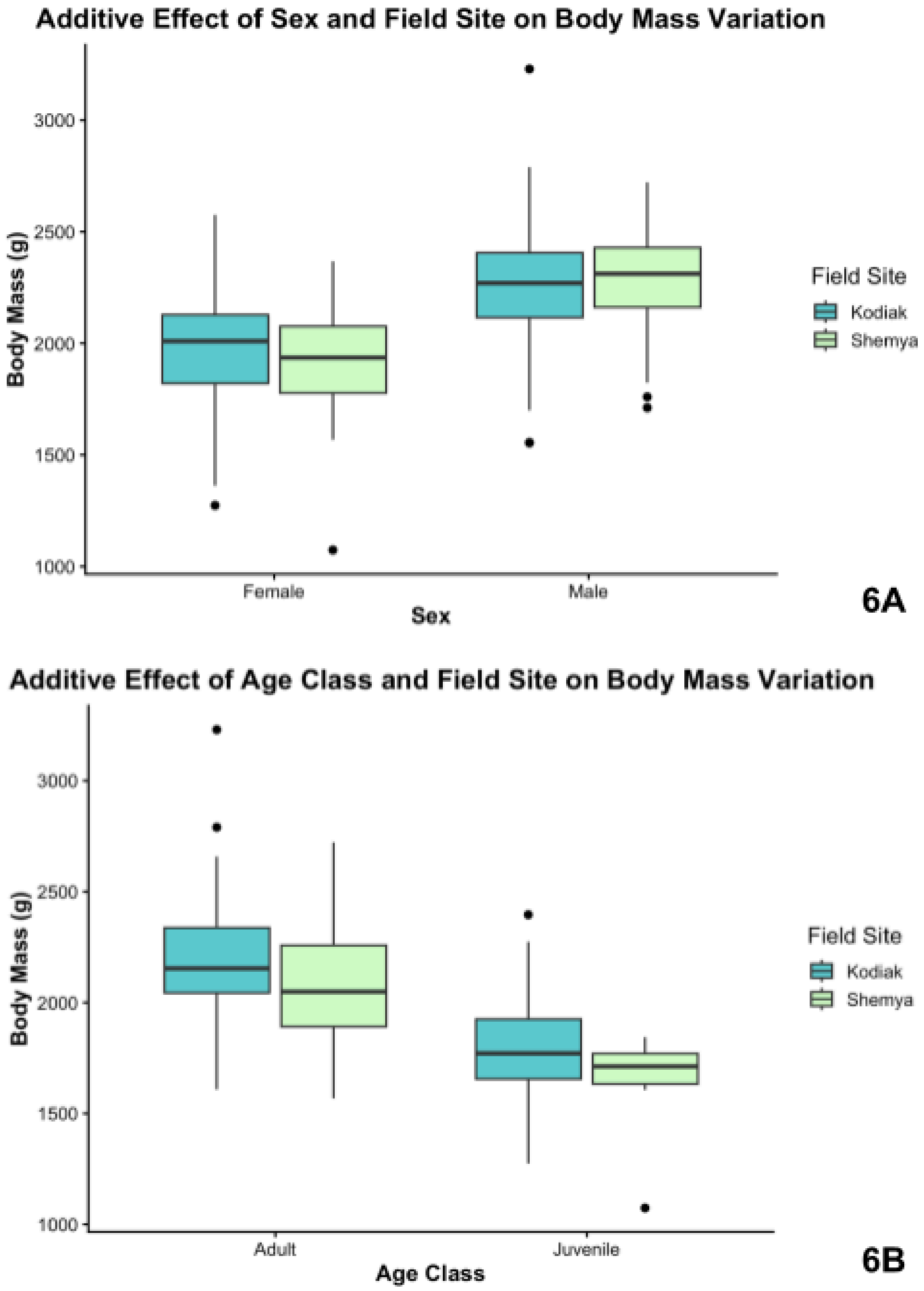


Figure 6A and 6B: These boxplots exhibit the additive effects of (**6A**) Sex and Field Site and (**6B**) Age Class and Field Site to explain variation in body mass, as displayed in the most parsimonious model (lm(A+S+FS)). These boxplots are directly plotted from the model lm(A+S+FS) and loosely demonstrate the additive effects of sex, age class, and field site on emperor goose body mass.

Additionally, given the observed significant difference in adult female body mass between the two different wintering sites, it would be interesting to conduct a study that investigates potential differences in nesting behavior and recruitment, as well as overall reproductive success rates between females that winter at Shemya versus Kodiak. For emperor geese females, who are particularly attentive to nests during incubation periods, it is extremely important that they accumulate and maintain high levels of endogenous reserves during the winter in order to be prepared to breed once they reach breeding/nesting grounds in the summer (Thompson and Raveling 1987). According to the results of this study, emperor geese females that wintered on Shemya are significantly lighter, potentially indicating lower levels of endogenous reserves. Thus it could be interesting to investigate whether nesting success and incubation behaviors differ between emperor geese that winter at Shemya versus emperor geese that winter at Kodiak (Schmutz et al. 2006).

In order to properly conserve and manage emperor goose populations, especially in light of recent population fluctuations, it is extremely important to study them throughout their year-round cycle. This is especially the case during times of the year where they are understudied, such as their wintering grounds where they spend approximately half of their lives (Pacific Flyway Council 2016). The conditions that waterfowl experience at their wintering habitats can have severe impacts on their reproduction and survival (Sedinger and Alisauskas 2014). Therefore, understanding winter conditions at wintering sites and how those affect the fitness of individual emperor geese, can help improve estimates of body condition, survival, recruitment, and overall population growth projections, providing information that is imperative for deriving appropriate hunting quotas and restrictions (Sedinger and Alisauskas 2014).

In the context of recent and historical rapid declines in emperor goose populations, it is more important than ever to design conservation and management plans that account for the entire span of the emperor goose life cycle, including wintering habits and habitats. The findings from this study suggest that potential conservation efforts need to be focused on Shemya in order to bolster the fitness of geese, especially female geese, on Shemya. Potentially more strict hunting regulations could be placed on hunting emperor geese that winter Shemya Island where emperor geese populations are already struggling due to physiological stressors and supplemental feeding could be used to ensure adult emperor geese that winter on Shemya have proper endogenous reserves to survive through the winter, complete the long migration to and from wintering sites, and successfully raise offspring in the summer. The findings of this study also emphasize the importance of Kodiak in providing optimal wintering habitat for emperor geese and show that Kodiak needs to be protected as a form of refugia for emperor geese populations. Therefore, strict hunting restrictions and limits on human development should be implemented to protect these wintering grounds on Kodiak for emperor geese populations. Further exploring heterogeneity in the wintering distributions of emperor geese and correlating variation in fitness of individuals is crucial for understanding why emperor goose populations have been struggling and creating intentional and effective management plans that protect this species of cultural, recreational, and ecological significance.

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