

Activity budgets of inland versus coastal *Larus argentatus* populations in Maine

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Abstract

Comparing the behavior of wildlife populations residing in different habitats can give insight into external factors that influence behavior and explain why certain behaviors are exhibited by a species. In this study, we compared the average activity budgets of Herring Gulls (*Larus argentatus*) residing around inland and coastal habitats. We hypothesized that gulls in inland settings would be more likely to exhibit inactive behaviors such as loafing and sleeping, while gulls in coastal settings would exhibit more active behaviors such as foraging, walking, and squabbling. We observed a total of 100 individual gulls throughout the state of Maine, with 50 found inland and 50 on the coast. Behaviors exhibited by individuals were recorded in fifteen-second intervals throughout the span of five-minutes, which were then averaged for each population to generate average time budgets for inland and coastal gulls. Statistical analysis revealed that time spent performing loafing, sleeping, walking, and foraging behaviors were statistically different between the two populations while time spent performing self-maintenance, scouting, and anxious behaviors were not statistically different. We found that coastal gulls spent more time foraging, while inland gulls spent more time exhibiting loafing behaviors. Our results support the hypothesis

that inland gulls perform inactive behaviors at a higher rate than coastal gulls, and conversely coastal gulls perform active behaviors at a higher rate than inland gulls.

Keywords: *Larus argentatus*, Herring Gull(s), ethogram, ethology, behavior, activity budget, inland, coastal, urban, rural, attentive, aggressive, agitated, comfort, self maintenance

Introduction

The study of ethology has historically allowed researchers to identify patterns in animal behavior and hypothesize about adaptations that have arisen in observed species (Miller 1988). The ability to draw conclusions about why certain behaviors are performed and identify the underlying mechanisms behind them relies on comparative observation between conspecific populations (Miller 1988). Herring Gull (*Larus argentatus*) were among the first species whose behavior was observed and documented due to the species' abundance, accessibility, and easily observed movements (Tinbergen 1954). Since the advent of these early foundational studies on Herring Gull behavior, more recent literature has proceeded to not just observe gulls, but also quantify behavioral observations to compare and contrast the ethology and time budgets of conspecific populations. *Larus argentatus* is comfortable with taking advantage of both human food-waste and intertidal prey in natural coastal environments, but the influence of human-presence on the behavior of the Herring Gull has not yet been extensively explored in literature thus far (Furst et al. 2018). Herring Gull in urban populations exhibit reduced defensive behaviors towards humans than their rural counterparts, but little is known about the impact that humans have on overall behavioral trends (Goumas et al. 2020). However, anthropogenic presence and

development have been found to impact the ethology and ecology of similar gull species (Feng & Liang 2020; Pierotti & Annett 1991, 2001; Wells 1994). Black-headed Gulls (*Chroicocephalus ridibundus*) in urban environments were observed exhibiting behaviors correlated with domestication, displaying fewer defensive postures and traveling shorter distances to forage than their rural counterparts (Feng & Liang 2020). Additionally, diet choice and nest-site selection significantly differ between urban and non-urban Herring Gull, Western Gull (*Larus occidentalis*) and Great Black-Backed Gull (*Larus marinus*) populations (Pierotti & Annett 1991, 2001; Wells 1994). These findings led us to hypothesize that Herring Gull in inland settings would be more likely to exhibit inactive behaviors, while gulls in coastal settings would exhibit more active behaviors due to differences in caloric and nutrient availability, as well as the effort required for each population to attain food in their respective environments. The objective of our study was to determine if the time budget of inland and coastal gulls differed from one another, as well as to make an ethogram of common behaviors of the gulls observed in the two distinct habitats.

METHODS

Study Area

Inland gulls were observed in Orono, Maine from mid-February to mid-March between the hours of 8:00am-12:00pm on the University of Maine campus and the local strip mall parking lot behind a Wendy's fast-food restaurant. Coastal gulls were also observed from mid-February to mid-March, during low tide on beaches and intertidal zones in Cherryfield, Machias, Milbridge, Ellsworth, and Wells, Maine.

Data Collection and Analysis

Over the two-month period that the study was conducted, we observed and recorded the behaviors of one hundred total individual Herring Gull, fifty from each population. We observed each individual over a five minute span and recorded the most prominent behavior they exhibited in fifteen-second intervals. Since no gull was individually marked, when two observers were watching a given population at the same time, we made sure that neither observer was watching the same individual at the same interval by pointing out which exact gull we were observing, and by starting at opposite ends of the distribution of individuals over the landscape. We operated under the assumption that an individual gull under observation could successfully be followed via binoculars for the duration of the five-minute behavior-recording period.

Our data sheet included space for recording the date and time, the time of each interval in minutes and seconds, the behavior exhibited during each interval, observer initials, location, weather summations, and the time of low tide that day (Dockery & Reiss 1996). We followed this same methodology for recording behavior at every inland and coastal site, which we initially selected by being able to visually locate and safely observe groups of twenty to upwards of one hundred Herring Gull at a time.

After collecting data on both gull populations, we generated an ethogram of all observed behaviors using previously published descriptions of gull ethology as a foundation (Hand et al. 1985; Tinbergen 1953). Behaviors were placed in one of four categories: attentive, aggressive, inactive or comfort, and active (Table 1; Hand et al. 1985; Tinbergen 1953). Attentive behavior included wary or anxious actions such as visually scouting an area, flying and circling around a perimeter, or holding an anxiety posture

(Table 1; Hand et al. 1985; Tinbergen 1953). Aggressive behavior was defined as squabbling, maintaining a threat posture, or producing a defensive vocalization (Table 1; Hand et al. 1985; Tinbergen 1953). Inactive or comfort behavior included preening, stretching, feather-shaking, loafing, scratching, or sleeping (Table 1). Lastly, active behavior included foraging, eating, and walking (Table 1; Hand et al. 1985; Tinbergen 1953). For the purpose of statistical analysis, some behaviors were combined under one label. Comfort activities such as preening, feather-shaking, stretching, and scratching were combined under the label “self-maintenance” in figures; anxiety and threat postures, flying and circling, and defensive vocalizations were combined under the label “anxious behaviors” in figures.

We calculated the frequency of each behavior per individual and averaged them for both the inland and coastal populations. Then, we created a clustered column chart to compare the frequency of each behavior between the inland and coastal Herring Gull populations (Figure 1). We also generated a pie chart for both the inland and coastal population to determine the average activity budget for an individual gull residing in each habitat-type (Figure 3). We used the data to conduct a *t*-test to determine if the frequency of each behavior in coastal and inland locations significantly differed from one another (Table 2).

Results

A series of *t*-tests revealed that there was a significant difference in time spent loafing, sleeping, walking, and foraging between inland and coastal gulls (Table 2; Figure 1). Inland gulls spent significantly more time loafing ($M = 12.10$, $SD = 6.925$), than coastal gulls ($M = 2.41$, $SD = 4.785$); $t(98) = 8.199$, $p < .0001$ (Table 2; Figure 1). The inland population ($M = 1.68$, $SD = 3.777$) was also found to sleep more than the coastal population ($M =$

0.260, $SD = 1.838$); $t(98) = 2.39$, $p = 0.0187$ (Table 2; Figure 1). Coastal gulls displayed higher rates of active behavior than inland gulls. The coastal population ($M = 6.90$, $SD = 7.959$) foraged more than the inland population ($M = 0.50$, $SD = 1.374$); $t(98) = 5.603$, $p = 0.0001$ (Table 2; Figure 1). The coastal population ($M = 1.50$, $SD = 2.332$) also walked more frequently than the inland population ($M = 0.24$, $SD = 0.0005$); $t(98) = 3.627$, $p = 0.0005$ (Table 2; Figure 1). No significance was found between the two populations when comparing time spent performing self-maintenance, anxious behaviors, and scouting (Table 2). When directly comparing inactive to active behaviors exhibited by each population, inland gulls were observed performing more inactive behaviors and less active behaviors, while coastal gulls were observed performing more active behaviors than inactive behaviors (Figure 2).

Pie charts displayed the total percentage of time budgeted towards each activity for each population. The inland Herring Gull population spent 59.5% of their time loafing compared to 11.7% in coastal gulls (Figure 3). Coastal gulls spent 33.8% of their time foraging compared to 2.5% in inland gulls (Figure 3).

DISCUSSION

Mechanisms

In this study we investigated the hypothesis that inland Herring Gull would exhibit more inactive behaviors than coastal Herring Gull, who would conversely exhibit more active behaviors. We found strong evidence to support this hypothesis in our investigation. Inland gulls loafed and slept significantly more than coastal gulls, while coastal gulls foraged and walked significantly more than inland gulls. These differences in the activity budgets

between the two populations may be attributed to the quantity and quality of food available as well as amount of competition for resources in each environment. Individual gulls tend to specialize in foraging for either intertidal organisms or anthropogenic refuse, and there is a cost-benefit tradeoff associated with each type of specialization (Donk et al. 2017, Pierotti & Annett 2001). Intertidal prey are found in small quantities that are nutritionally dense and reliably found. However, intertidal organisms contain large amounts of indigestible remains and are energetically costly to forage for (Donk et al. 2017). Inland gulls have the opportunity to acquire large amounts of food in a single sitting with lower bouts of energy invested in foraging. Despite this food-source being higher-calorie than natural prey, human refuse is less nutritious and less predictable to encounter than intertidal meals (Donk et al. 2017).

The different tradeoffs that an individual must make for acquiring energy in each habitat type has a direct effect on Herring Gull behavioral patterns. Time spent foraging and total energy intake is determined by an individual's energy return on investment (EROI). EROI is the ratio of the amount of usable energy an organism gains from performing an action to the energy it exerted when performing said action (Hall 2017). The maximization of EROI drives all behavioral patterns observed in a species because a surplus of energy is required to survive and reproduce (Hall 2017). Due to a disparity in the quantity and quality of available resources in the inland versus coastal environment, individuals must behave differently in these environments to achieve the same EROI. Coastal gulls obtain small amounts of low-calorie, high quality food, but exert more energy to attain this food due to the required investment in frequent active-foraging behaviors. Conversely, inland gulls were presumed to intake large amounts of high-calorie, lower quality energy during

each feeding period, and therefore only need to expend the energy they acquired in less frequent, more aggressive bursts. The excess surplus energy is likely why inland gulls were observed exhibiting more restful behaviors such as sleeping and loafing. Since food of anthropogenic origin is extremely energy dense for its small volume and does not require extensive searching to find, inland gulls can afford to exhibit more behaviors that would be accretive to long periods of inactivity (Hall 2017).

Although the higher caloric intake of the inland gulls allows them to be less active than coastal gulls overall, they have to spend more energy defending resources from conspecifics (Donk et al. 2019). We observed this anecdotally while gathering data, as there were frequent anxious and aggressive behaviors such as squabbling exhibited towards conspecifics over limited food resources in the densely populated areas near fast food chains. The coastal gulls exhibited competition for resources as well, although individuals were more evenly distributed over the intertidal spaces they foraged in. This is a direct result of prey selection based on the energetic profitability of each prey type, or rather, the energy return on investment of the prey for the individual (Suraci & Dill 2011). High-calorie food is more valuable to an individual, so they are more likely to defend it from other conspecifics to gain fitness advantages.

Another pressure that likely influenced the behavioral differences observed between inland and coastal Herring Gull populations was the amount of interspecific competition present, especially with gull species of larger stature. In mixed flocks where foraging grounds are densely populated, Great Black-Backed Gull (*Larus marinus*) have been observed aggressively suppressing Herring Gull to such an extent that in some cases the latter was pushed out of the foraging grounds entirely (Rome & Ellis 2004). Due to the high amount of interspecific competition,

Herring Gull may be deterred from choosing the more nutrient-rich coastal habitat for foraging, as it would cost them less energy to move inland for high-calorie food sources rather than compete with a species larger than themselves for low-calorie food sources. This dynamic would also push outcompeted gulls into more inland foraging grounds, therefore increasing the amount of intraspecific competition for those limited resources until the Great Black-Backed Gulls abandon their feeding grounds for the breeding season (Rome & Ellis 2004).

Conclusion and Future Directions

Our study suggests that the activity budgets of inland and coastal Herring Gull populations in Maine differ from one another. However, this conclusion was drawn from data collected in a limited timeframe, so extending this study would solidify these results and improve the study design. This could be accomplished by collecting behavioral data over the span of several years, seasons, and times rather than just a couple of months. To further improve the study design and make a more streamline process for observers, the inclusion of the software ‘JWatcher’, produced by Daniel T. Blumstein, Janice C. Daniel, and Christopher S. Evans, would also be considered to more accurately record behaviors in real time, rather than the use of paper charts and stopwatches as used for this study. Despite these improvements that could be made to the study design, this work may act as preliminary research for larger-scale investigations regarding the mechanisms behind these differences as well as the consequences of them.

Some points of bias that stemmed from our study had to do with timing of observations, as well as keeping track of each of the individual gulls that were chosen by the observers. Since the gull in Machias, Cherryfield, Milbridge, and Schoodic byway were

only observed during low tides, the results for proportions of time spent exhibiting walking and foraging behaviors would be skewed higher compared to the inland gull at the same time.

In a paper looking at optimal foraging theory of black-billed gulls (*Chroicocephalus bulleri*), they examined models showing how this species tend to forage at sites close to colonies when available, with the highest distance from the colony being 11.9 km (7.4 mi) and a mean distance of 4.7 km (2.9 mi) (Evans 1982). This observation is backed by another paper where scientists looked at breeding herring gulls on islands in the German Wadden Sea, where each island was increasingly farther from the mainland (Enners et al. 2018). They also found that these gulls were more likely to take shorter trips to forage for food the further they were from the mainland, but mainland foraging was mostly for earthworms rather than human refuse (Enners et al. 2018). Based on these previous studies, it is entirely possible that similar individuals that were observed foraging inland could also be on the coast, and additional research and accommodations to the analyses of the data would have to be made to account for the variation between observed populations. There has not been much literature published on optimal foraging theory based on timing of foraging for inland gulls, and most of the literature that does look at the optimal foraging of various gull species looks specifically at the breeding and chick-rearing season, rather than the non-breeding, winter season of which this study in Maine had taken place.

Additionally, to account for the error in this study, each population would need to be observed both at incoming and outgoing tides to account for this error. Additionally, it was impossible for observers to keep an accurate account of which individuals had already been observed, as on about half of the occasions, something would startle the flock of gulls and they would flush, only to settle a few minutes later. In future studies

with optimal conditions and funding, either capture-mark-recapture methodology should be used, or the use of one observer per site and only one visit to each site would be permitted. During this study to account for this error as best as possible, each observer made sure to not observe the same bird in the same observation period, making sure to view opposite sides of the flock when observing in a pair.

For this study, observers made the assumption that coastal herring gulls stayed on the coast and did not travel inland to forage during the day, as well as the same assumption but inverted for inland gulls, although this assumption would need to be verified in future studies using capture-mark-resighting methodologies to confirm and eliminate biases of this aspect. Further research is also required to understand if the observed differences in time budgets of Herring Gull populations would also lead to disparities in aspects of their life history, such as the longevity and reproduction success of populations in each habitat. This has been briefly explored in a handful of studies, in which it was found that both rural Western and Herring Gull were more successful at hatching and raising chicks than their urban counterparts, which may be linked to the nutritional content of anthropogenic food (Pierotti & Annette 1991, 2001). In humans, a diet high in saturated fat has been found to alter the brain and bodily chemistry, leading to health issues such as insulin resistance, sluggish behaviors, and increased risk of heart disease (Kahn & Flier 2000). We speculate that a similar effect may be present in gulls who eat high amounts of fast-food refuse, which leads to lower fitness in urban gulls. Additionally, the effects of toxin bioaccumulation caused by gulls consuming human food additives could be explored. Recent isotope analyses have found higher levels of damage to the DNA in urban gulls than rural gulls, which may be linked to a diet composed of anthropogenic refuse (Keilen 2017).

Acquiring further evidence to either support or contradict these findings would expand the breadth of knowledge currently known about anthropogenic impact on avian behavior and life history. Since the management of anthropogenic resources is constantly changing, the costs and benefits of Herring Gull exploiting these resources continuously change as well (Donk et al. 2019, O’Hanlan & Nager 2018). These dynamic shifts through space and time leave open a window of opportunity to study and understand the effects that urbanization has on avian populations.

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TABLES & FIGURES

Table 1. Ethogram of behaviors observed in *Larus argentatus* from February 2021 to March 2021 in Maine, USA based on prior studies on gull behavior (Tinbergen 1954).

Category	Behavior	Description
Attentive	Scouting	Standing up and moving head side to side, surveying surroundings
	Anxiety posture	Body held tensely up with the neck held out and upright, and the head pointing up
	Flying and circling	Takes off in flight, circles a brief perimeter and lands again
Aggressive	Squabbling	Fighting with another gull or intimidating them
	Upright threat posture	Body held tensely up with the neck held out, and head pointing down
	Defensive vocalization	Posturing or squabbling, bird releases a long, drawn out warning call
Inactive or comfort	Preening	Bill makes contact with ventral feathers, over the shoulder or wing, and head shakes during contact
	Stretching	Wings or body elongated briefly, followed by a head or feather shake
	Feather shaking	Head or body briefly shaken vigorously side-to-side
	Loafing	Sitting down/ standing up with eyes open, passive gaze forward, yawns .
	Scratching	Foot makes contact with head or body to scratch an itch
	Sleeping	Sitting down with eyes closed
	Active	Foraging/eating
Walking		Traveling from one nearby location to another on the ground

Table 2. *T*-test results comparing the amount of time that inland and coastal populations of *Larus argentatus* spent performing behaviors in Maine, February-March 2021.

Behavior	Habitat	N	Mean	SD	Df	t	p	Outcome
Loafing	Inland	50	12.10	6.925	98	8.199	<.0001	Significant
	Coastal	50	2.41	4.785				
Sleeping	Inland	50	1.68	3.777	98	2.39	0.0187	Significant
	Coastal	50	0.260	1.838				
Self-maintenance	Inland	50	2.88	4.736	98	1.52	0.1317	Not significant
	Coastal	50	4.60	6.449				
Scouting	Inland	50	1.88	4.711	98	0.301	0.3011	Not significant
	Coastal	50	3.76	11.889				
Walking	Inland	50	0.24	0.771	98	3.627	0.0005	Significant
	Coastal	50	1.50	2.332				
Foraging	Inland	50	0.50	1.374	98	5.603	0.0001	Significant
	Coastal	50	6.90	7.959				
Anxious behaviors	Inland	50	1.08	2.617	98	0.092	0.4636	Not significant
	Coastal	50	2.44	4.999				
$p \leq 0.05$								

Figure 1. A comparison of behavior frequency observed in *Larus argentatus* in inland settings versus coastal settings from February 2021 to March 2021 in Maine, USA.

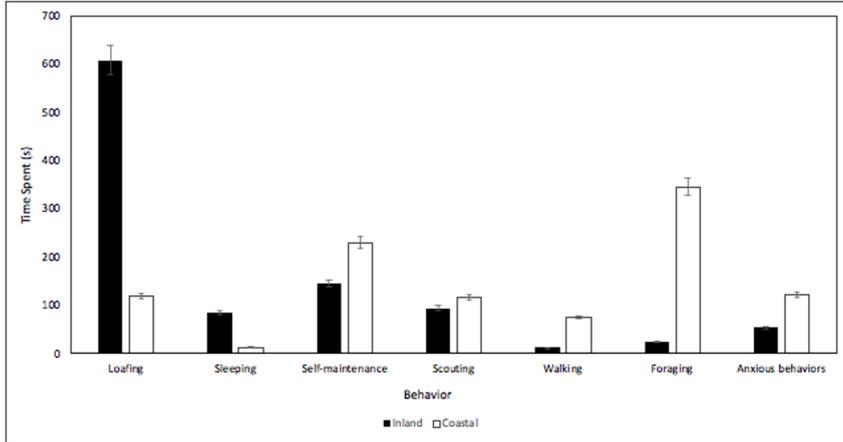
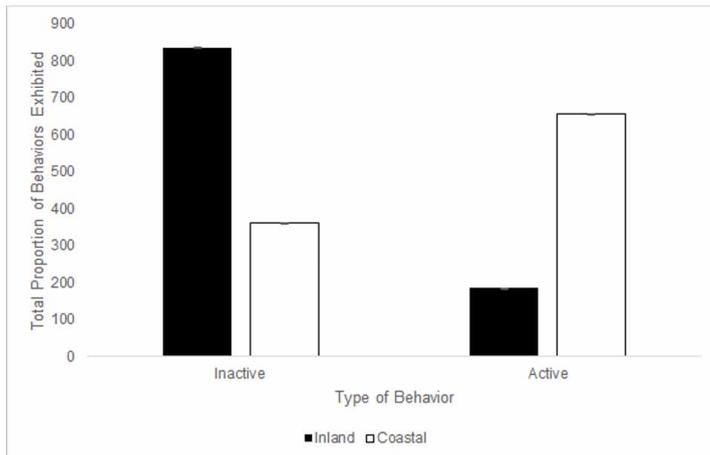


Figure 2. A comparison of type of behavior frequency observed in *Larus argentatus* in inland settings versus coastal settings from February 2021 to March 2021 in Maine, USA. Inactive behaviors consist of loafing, sleeping, and self-maintenance, while active behaviors consist of scouting, walking, foraging, and anxious behaviors.



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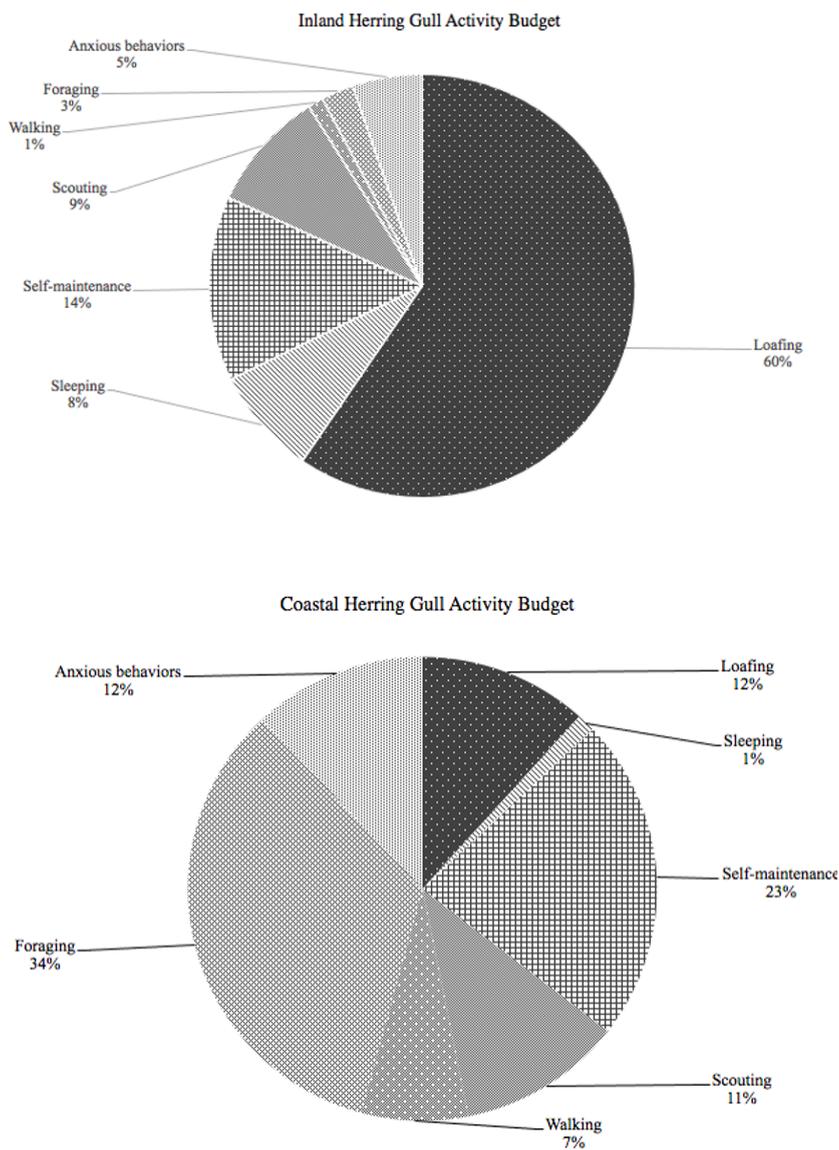


Figure 2. Comparison of average time budget per individual *Larus argentatus* in inland settings versus coastal settings from February 2021 to March 2021 in Maine, USA.