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ARTICLE

Foraging behaviour of four avian species feeding on the same temporarily available prey

N.S.B. Houpt, A.P.H. Bose, T. Warriner, N.A.W. Brown, J.S. Quinn, and S. Balshine

Abstract: Low tide events provide terrestrial predators with ephemeral, but predictable and abundant sources of prey. Understanding the relationships between tidal cycles, prey availability, and predator abundances is vital to characterizing the ecological relationship between terrestrial predators and their marine prey. Here, we describe the foraging tactics of four common bird species in western North America — Bald Eagles (*Haliaeetus leucocephalus* (Linnaeus, 1766)), Great Blue Herons (*Ardea herodias* Linnaeus, 1758), Glaucous-winged Gulls (*Larus glaucescens* J.F. Naumann, 1840), and Northwestern Crows (*Corvus caurinus* S.F. Baird, 1858) — feeding on the same transiently accessible fish species, the plainfin midshipman (*Porichthys notatus* Girard, 1854). We conducted avian predator surveys at breeding beaches of plainfin midshipman across multiple years and sites. Our census data showed that Bald Eagle and Great Blue Heron abundances were higher when the tides were receding than incoming at Ladysmith Harbour, British Columbia, Canada, but the opposite trend was found for total predator abundance at a second site in Dabob Bay, Washington, USA. Glaucous-winged Gull abundance decreased over the course of the plainfin midshipman breeding season (April–July), whereas the abundances of the other three species remained stable. Our data suggest that the foraging activities of birds in the intertidal zones of western North America are linked with the tidal cycles, corresponding to periods of high prey vulnerability.

Key words: hunting, intertidal zone, optimal foraging, partial prey consumption, predator distribution.

Résumé : Les épisodes de marée basse fournissent à des prédateurs terrestres des sources de proies éphémères, mais prévisibles et abondantes. La compréhension des liens entre les cycles des marées, la disponibilité de proies et l'abondance de prédateurs est essentielle à la caractérisation de la relation écologique entre les prédateurs terrestres et leurs proies marines. Nous décrivons les stratégies d'approvisionnement de quatre espèces d'oiseaux répandues dans l'ouest de l'Amérique du Nord — le pygargue à tête blanche (*Haliaeetus leucocephalus* (Linnaeus, 1766)), le grand héron (*Ardea herodias* Linnaeus, 1758), le goéland à ailes grises (*Larus glaucescens* J.F. Naumann, 1840) et la corneille d'Alaska (*Corvus caurinus* S.F. Baird, 1858) — qui se nourrissent de la même espèce de poisson accessible de manière intermittente, le pilotin tacheté (*Porichthys notatus* Girard, 1854). Nous avons réalisé des recensements de prédateurs aviens sur des plages de reproduction des pilotins tachetés sur plusieurs années et en plusieurs lieux. Nos données de recensement montrent que les abondances des pygargues à tête blanche et des grands hérons sont plus élevées à marée descendante qu'à marée montante dans le havre de Ladysmith (Colombie-Britannique, Canada), alors que la tendance inverse est observée pour ce qui est de l'abondance totale de prédateurs dans un deuxième site dans la baie de Dabob (Washington, États-Unis). L'abondance des goélands à ailes grises diminue au fil de la saison de reproduction des pilotins tachetés (avril à juillet), alors que les abondances des trois autres espèces demeurent stables. Nos données donnent à penser que les activités d'approvisionnement des oiseaux dans les zones intertidales de l'ouest de l'Amérique du Nord sont reliées aux cycles des marées, correspondant à des périodes de grande vulnérabilité des proies. [Traduit par la Rédaction]

Mots-clés : chasse, zone intertidale, approvisionnement optimal, consommation partielle de proies, répartition des prédateurs.

Introduction

> *There are good things to see in the tide pools and there are exciting and interesting thoughts to be generated from the seeing. Every new eye applied to the peep hole which looks out at the world may fish in some new beauty and some new pattern, and the world of the human mind must be enriched by such fishing.* (John Steinbeck in Ricketts and Calvin 1948, p. xi)

American author John Steinbeck wrote these words as part of the preface to Ricketts and Calvin's (1948) classic *Between Pacific Tides* as a call to curious adventurers to visit and observe the diversity of life revealed in Pacific intertidal zones by the receding tides. Those that followed Steinbeck's advice would quickly find that the intertidal zone is a dynamic and productive ecosystem that hosts an incredible diversity of organisms (Pfister 2007; Seitz

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et al. 2014). However, the diversity and abundance of life visible at low tide attracts more than naturalists when the tides recede; a low tide event can also attract terrestrial predators by providing them with abundant, easily accessible prey, such as sessile molluscs, crustaceans, echinoderms, and even fish that become exposed or trapped by the receding tides (Bonesi et al. 2000; Smith and Partridge 2004). Although intertidal food sources are only intermittently available for terrestrial predators, their availability is predictable due to the periodicities of the tides. The daily (diurnal) and biweekly (lunar) tidal cycles provide limited but predictable foraging periods that can shape the foraging behaviours of terrestrial and avian predators (Recher 1966; Connors et al. 1980; Fleischer 1983; Hunt et al. 1998; Calle et al. 2016; Fonseca et al. 2017; Thorne et al. 2019). For example, on a diurnal scale, Ruddy Turnstones (*Arenaria interpres* (Linnaeus, 1758)) increase foraging activity in Costa Rican tidal flats near low tide and are more abundant when the tide is incoming (flooding) than receding (ebbing) (Fleischer 1983). Across lunar scales, coastal shorebirds increase in abundance in coastal lagoons in northwestern Mexico during the spring low tides, when the low water levels reveal a larger foraging habitat relative to neap tides (Fonseca et al. 2017). In this study, we investigated how the presence of four avian predators common to rocky intertidal beaches of western North America — Bald Eagles (*Haliaeetus leucocephalus* (Linnaeus, 1766)), Great Blue Herons (*Ardea herodias* Linnaeus, 1758), Glaucous-winged Gulls (*Larus glaucescens* J.F. Naumann, 1840), and Northwestern Crows (*Corvus caurinus* S.F. Baird, 1858) — varied with both diurnal and lunar tidal cycles when foraging on a transient prey source, the plainfin midshipman (*Porichthys notatus* Girard, 1854).

The plainfin midshipman is a species of toadfish commonly found in the rocky intertidal zones along the west coast of North America and is a major prey item for numerous species of birds (e.g., Bald Eagles: Elliott et al. 2003; Great Blue Herons: Forbes 1982; Western Gulls, *Larus occidentalis* Audubon, 1839: Spear 1993) and mammals (e.g., river otters, *Lontra canadensis* (Schreber, 1777): Guertin et al. 2010; harbour seals, *Phoca vitulina* Linnaeus, 1758: Luxa and Acevedo-Gutiérrez 2013). In late April and early May, plainfin midshipman migrate from depths of approximately 200–300 m to the shallow intertidal zone of rocky beaches (Figs. 1*a* and 1*b*). The relatively large males come to shore first and excavate nests under rocks, where they breed and care for offspring (Arora 1948; Brantley and Bass 1994; Sisneros et al. 2004). These males provide sole paternal care for the young for approximately 60 days (Cogliati et al. 2013) and remain in their nest even when it is exposed above the waterline by the receding tides (Arora 1948). Because egg-laying can take ≈20 h (Brantley and Bass 1994), spawning females can also become trapped in the nest cavities during low tide and must await the returning flood tide before they can swim back to the ocean. During low tide events, avian predators gain increased access to both sexes of plainfin midshipman while the fish swim between nests or are stranded in their nesting cavities above the waterline (Fig. 1*c*). Because these fish are an important food source for several terrestrial predators (Forbes 1982; Spear 1993; Elliott et al. 2003), but are transiently accessible, the plainfin midshipman offers a unique opportunity to study how foraging activities of multiple terrestrial species are governed by tidal periodicities.

Based on daily censuses collected over six breeding seasons, we quantified bird abundance patterns during spring low tides at a well-known plainfin midshipman spawning ground in British Columbia, Canada. We then supplemented this data by quantifying bird abundances across all phases of the tidal cycle at a second site in Washington, USA. Additionally, we conducted focal observations over seven breeding seasons at four plainfin midshipman spawning sites to better understand the similarities and differences in hunting tactics and prey handling behaviours employed by Bald Eagles, Great Blue Herons, Glaucous-winged Gulls, and Northwestern Crows (the four most common avian predators at our study areas) when capturing and consuming plainfin midshipman. Our results describe the temporal distribution of these four common predators across the diurnal and lunar tidal cycles and how their foraging behaviours are differentially affected by transience in prey accessibility.

Materials and methods

Intertidal field sites

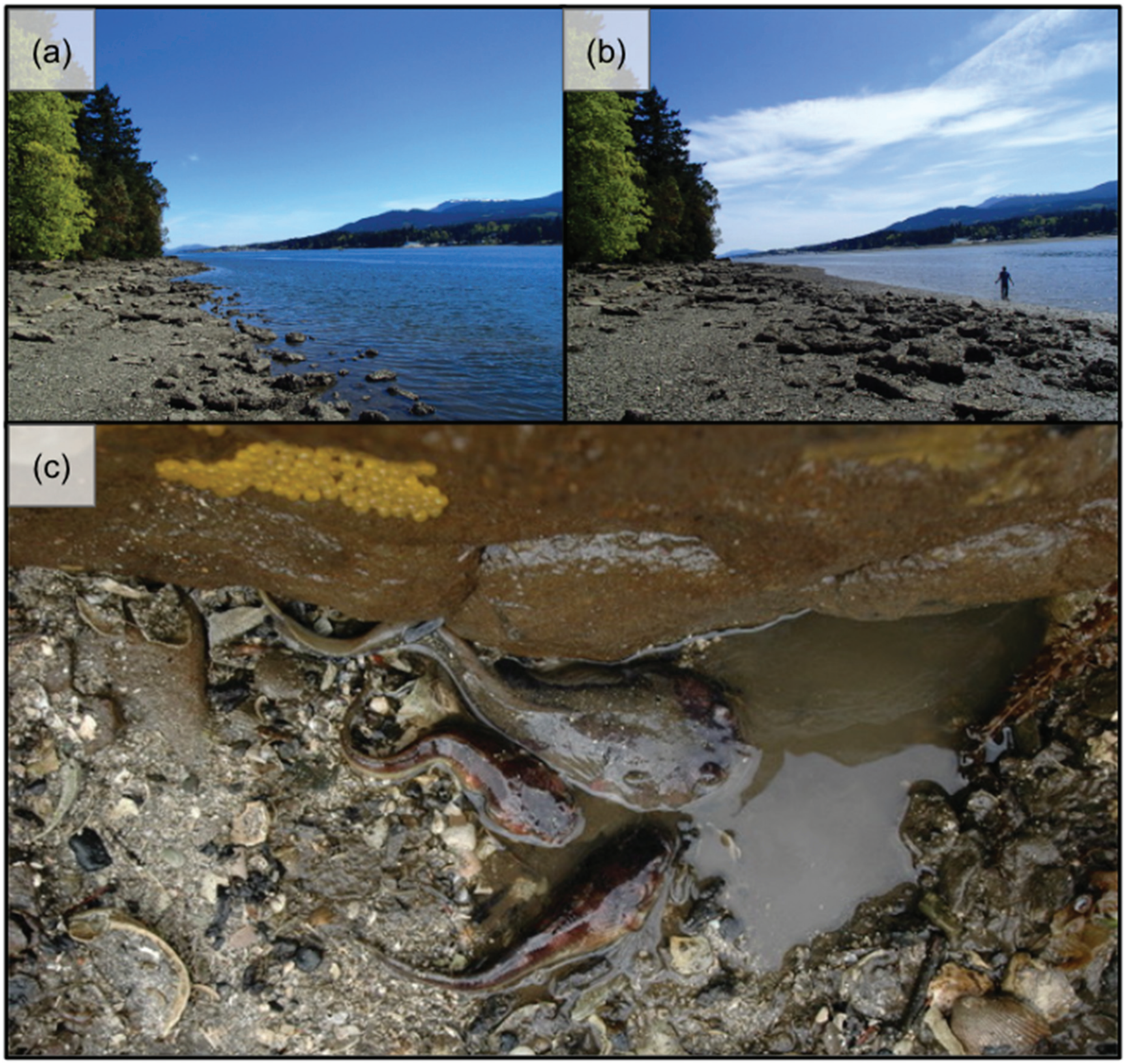
We collected abundance and behavioural data on Bald Eagles, Great Blue Herons, Glaucous-winged Gulls, and Northwestern Crows using census counts and focal follows during the 2011 and the 2014–2019 plainfin midshipman breeding seasons (April–August) at four different sites: Crescent Beach, British Columbia, Canada (49°01′27″N, 122°51′48″W), head of Ladysmith Harbour, British Columbia, Canada (49°01′15″N, 123°50′28″W), Holland Bank, Ladysmith Harbour, British Columbia, Canada (48°58′50″N, 123°48′07″W), and at a private beach located in Dabob Bay, Washington, USA (47°45′23″N, 122°51′02″W). Each site consisted of a rocky beach descending into a seagrass bed and all sites were located on the west coast of North America. In this region, coasts experience mixed semidiurnal tides, meaning two high tides and two low tides of different magnitudes occur each lunar day. Behavioural observations were typically collected during the 6–10 days centered around one or both of each month's lowest spring tide events.

Temporal distribution of predators

Over these years we visited one field site most frequently: the head of Ladysmith Harbour. Here, our predator surveys were systematic and frequent, so we used these data to estimate bird abundances across three time scales: (1) the diurnal tidal cycle (bird abundances during the ebbing and flooding tides), (2) the lunar tidal cycle (bird abundances on days with different minimum low tides, corresponding to the position of the day within the lunar cycle), and (3) the plainfin midshipman breeding season (bird abundances varying from late April to early July). Surveys were conducted by standing at a high point on the beach and scanning 180° clockwise from the tree line, across the intertidal zone looking toward the water, and then back to the tree line on the other side of the observer. During each scan, the observer counted the total number of each of the four focal avian predators (Figs. 2*a*–2*d*). A confirmatory counterclockwise scan was conducted after the initial scan. Birds were only counted in the survey if they were within ≈90 m of the observer. We conducted 117 predator surveys across 86 days at Ladysmith Inlet during six plainfin midshipman breeding seasons (2011, 2014–2018; date range: 21 April to 19 July). Predator surveys were performed on arrival at the field site before we began working on the beach (our main study species is the plainfin midshipman), which usually occurred several hours before the lowest tide of each day. We also conducted predator surveys just before departing the site if human activity on the intertidal beach had been minimal. We did this to ensure that we excluded situations where bird abundance data was low because of human disturbance (Gordon and Bahls 2018). We used binoculars (Olympus 8 × 22 RCII) to identify each bird species. For each day that a predator survey was conducted, the times and heights of the maximum and minimum tide points at Ladysmith Harbour were recorded from an online tide chart (https://www.mobilegeographics.com; site: Ladysmith, British Columbia). The time of day that each predator scan was performed was then used to specify whether the survey was conducted during the receding or incoming tide.

The above-described predator surveys omitted days that were near to or coincided with the neap tides of each month. Therefore, to investigate how predator abundances changed across all phases of the lunar tidal cycle, we conducted predator scans of the four focal avian species from 23 April to 8 June 2019 at the field site in

Fig. 1. Example of a rocky intertidal zone at (*a*) high tide and (*b*) low tide. (*c*) An intertidal rock overturned at low tide to reveal a plainfin midshipman (*Porichthys notatus*) nesting cavity. The largest, topmost fish is the guarder male, whereas the other smaller fish are a female (lower) and sneaker male (middle). Note the yellow–orange eggs laid on the undersurface of the rock, which is also the roof of the nesting cavity (photographs courtesy and reproduced with permission of A.P.H. Bose and S. Balshine, Ladysmith, British Columbia, Canada). Colour version online.



Dabob Bay, Washington (77 scans over 44 days). Data were collected following the same protocol described above, but censuses spanned three spring and neap tidal cycles, including days when no plainfin midshipman nests were emersed at any time — the vast majority of plainfin midshipman nests are too low in tidal elevation to become exposed by the retreating waterline on days near the neap tides of each month. These censuses therefore allowed us to determine the extent to which avian predators feed at plainfin midshipman breeding grounds while the fish nests are completely submerged and prey are least accessible to the birds.

Descriptions of hunting and prey-handling behaviours of the four avian species

During the 2016–2019 plainfin midshipman breeding seasons, focal follows of the avian predators foraging in the intertidal zone were conducted during visits to four beaches (Ladysmith Harbour, Holland Bank, Crescent Beach, and Dabob Bay). Individual focal birds were chosen haphazardly while sitting at distances of 10–30 m away and remaining still. The behaviours exhibited by the focal bird were observed through binoculars (Olympus 8 × 22 RCII) and recorded continuously for 10 min, or until the focal bird moved out of sight. Descriptions of the searching, locomotion, striking, handling, and consumption behaviours of the four avian predators were recorded. Table 1 provides summary statistics of the number of each bird species observed, the observation time, and the number and rate of fish consumed.

In our focal observation periods, the plainfin midshipman was the only fish species that we observed being captured and consumed by the four focal predators. During low tides, plainfin midshipman were caught by birds while the fish swam in shallow water between rocks, or while they were trapped in a shallow tide pools, in a seagrass bed isolated from the ocean by the receding tide, or while they were inside a nesting cavity but with an emerging appendage (head, tail, or fin) that could be grasped by a predator. The avian predators exhibited four general types of foraging behaviours, which we termed "perched ground hunting", "aerial hunting", "hunting while swimming", and "hunting while wading". The specific handling and consumption behaviours performed by each predator are detailed in Table 2.

Fig. 2. Four species of avian piscivores hunting in the intertidal zone. (*a*) Bald Eagle (*Haliaeetus leucocephalus*) grasping a plainfin midshipman (*Porichthys notatus*) in its beak (photograph courtesy and reproduced with permission of D. Gluckman, Dabob Bay, Washington, USA). (*b*) Great Blue Heron (*Ardea herodias*) manipulating a large plainfin midshipman in its beak, moving it into the correct orientation before swallowing it headfirst (photograph courtesy and reproduced with permission of R.M. Harbo, Holland Bank, British Columbia, Canada). (*c*) Glaucous-winged Gull (*Larus glaucescens*) preparing to swallow a large plainfin midshipman (photograph courtesy and reproduced with permission of C. MacDonald, Chemainus, British Columbia, Canada). (*d*) Northwestern Crow (*Corvus caurinus*) removing the intestines of a small plainfin midshipman prior to removing and consuming its liver (photograph courtesy and reproduced with permission of R.M. Harbo). Colour version online.

Table 1. Summary information from 86 focal follows.

Species	No. of birds observed	Cumulative observation time (min)	No. of plainfin midshipman consumed	Rate of plainfin midshipman consumption (fish·bird^{-1}·h^{-1})
Bald Eagles	26	243.8	6	1.48
Great Blue Herons	20	167.7	11	3.94
Glaucous-winged Gulls	21	190.3	3	0.95
Northwestern Crows	19	113.2	9	4.77
Total	86	715	29	2.43

Note: Focal follows were conducted on Bald Eagles (*Haliaeetus leucocephalus*), Great Blue Herons (*Ardea herodias*), Glaucous-winged Gulls (*Larus glaucescens*), and Northwestern Crows (*Corvus caurinus*) feeding on plainfin midshipman (*Porichthys notatus*) recorded at four sites combined (i.e., head of Ladysmith Harbour (British Columbia, Canada), Holland Bank (British Columbia, Canada), Crescent Beach (British Columbia, Canada), and Dabob Bay (Washington, USA)).

Perched ground hunting was employed by all four predators and consisted of searching for exposed prey once the tide had receded. When employing perched ground hunting, birds moved around the intertidal zone by hopping or walking, moving between rocks until a fish was found accessible within a nesting cavity, confined to a shallow tide pool, or beached and exposed on the sand, rock, eelgrass (*Zostera marina* L.), or mud flat. Once a fish had been spotted, the predator walked or hopped toward it, captured it within its beak (all four bird species) or its claws or talons (Northwestern Crows and Bald Eagles only), and began handling before consuming the prey (handling behaviours are described in Table 2).

Table 2. Handling and consumption behaviours of four avian predators feeding on plainfin midshipman (*Porichthys notatus*) in rocky intertidal zones along the west coast of British Columbia, Canada, and Washington, USA.

	Bald Eagles (*Haliaeetus leucocephalus*)	Great Blue Herons (*Ardea herodias*)	Glaucous-winged Gulls (*Larus glaucescens*)	Northwestern Crows (*Corvus caurinus*)
Transport and handling behaviour	Prey is carried by beak or talons to a rocky perch on the beach or to a tree. Prey is often transferred between beak and talons during flight	Prey is dropped and picked up repeatedly in tide pools or the ocean. Birds often use their beaks to stab and subdue prey and reposition fish in beak frequently before consuming	Prey is transported to the shoreline and repeatedly dipped or dropped in the water and recaptured before consumption	Prey is transported by beak while flying or hopping along to a dry area of the intertidal zone
Consumption	Small fish are swallowed whole, headfirst. Large fish are pinned by the bird's talons, ripped apart, and swallowed in strips	Plainfin midshipman of all sizes are swallowed headfirst	Mainly small and medium-sized plainfin midshipman, but occasionally larger fish, are swallowed headfirst	Small and medium-sized plainfin midshipman are flipped onto their dorsal sides and then pinned to the ground with one claw. Prey is pecked repeatedly in the abdomen and organs within the body cavity are removed
Remains left behind	No remains of small fish are left behind. Parts of large fish's liver, intestinal tract, swim bladder, heart, testes, head, and skeleton are sometimes left behind	No prey remains are left behind	No prey remains are left behind	Virtually the entire intact carcass is left behind. Carcass always has a diagnostic hole in the upper or lower abdomen. Birds normally consume only the liver and the ovaries (if female), leaving the remaining carcass and organs behind. Sometimes the fish was not yet dead when left in this position and the bird would begin hunting again

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Aerial hunting was performed mainly by Bald Eagles. This maneuver involved flying above the beach and searching for plainfin midshipman that were swimming in shallow water. Once a fish was spotted, the predator would descend and capture the fish with its talons (Bald Eagles) or with its beak (Glaucous-winged Gulls) and then accelerate upward again.

Hunting while swimming was only employed by Glaucous-winged Gulls and began with the bird swimming close (2–3 m) to the shore and scanning down into the water. Once a prey item was spotted beneath the surface, the focal bird plunged its head and neck underwater 1–5 times. Successful Glaucous-winged Gulls emerged from the water with a plainfin midshipman in their beaks.

Hunting while wading was performed by Great Blue Herons only and began when a focal bird waded into a tide pool or shallow waters along the shoreline. Great Blue Herons remained still and searched for plainfin midshipman at the water's edge or while slowly walking through the tide pool. Fish hunted in this manner were always fully submerged. When a fish was spotted, Great Blue Herons walked toward it before striking; striking occurred with either an open or a closed beak to grasp or skewer the fish, respectively.

Statistical analyses

We used R version 3.6.0 (R Core Team 2019) to conduct all statistical analyses. We fit a generalized linear mixed-effects model (GLM) using R package lme4 (Bates et al. 2015) to the combined abundance (count) data of all bird species collected from the head of Ladysmith Harbour. Because our abundance data were overdispersed, our model assumed a generalized Poisson error distribution (Brooks et al. 2019). We included species as a fixed effect and day of year and the observation day's low tide height (in metres) as two continuous predictor variables. Day of year was included as a proxy for plainfin midshipman intertidal density, which decreases throughout their breeding season (Bose et al. 2014, 2018), whereas low tide height was included to model how prey abundance varied with the lunar tide cycle. We also included a predictor variable that categorized the tidal stage as either receding or incoming at the time of our observation to model diurnal tidal variation. Year and day ID (day of year nested within year) were included as random intercepts to account for days when multiple observations occurred. We fit a similar model to census data collected at Dabob Bay in 2019. However, instead of including low tide height as a fixed effect, we included a dichotomous variable — prey accessibility — according to whether the daily low tide reached ≤0.1 m (relative to chart datum), indicating if the highest intertidal plainfin midshipman nests were emersed for any duration of time (Bose et al. 2019). Fixed effects were species, prey availability (emersed or immersed), and day of year. Due to limited sample size at Dabob Bay, we did not include interaction terms between species and the other fixed effects. Day ID was included as a random intercept to account for days when multiple observations were recorded.

Results

Across all 117 censuses, we recorded a mean of 3.25 avian predators (median: 2; range: 0–13) at our study site at the head of Ladysmith Harbour on Vancouver Island. We recorded a mean of 0.63 (median: 0; range: 0–6) Bald Eagles, 1.31 (median: 1; range: 0–8) Great Blue Herons, 1.09 (median: 0; range: 0–12) Glaucous-winged Gulls, and 0.21 (median: 0; range: 0–2) Northwestern Crows. Overall predator abundance did not differ clearly between receding and incoming tides (GLM, $\chi^2_{[3]} = 3.22$, $P = 0.073$); however, the effect of receding vs. incoming tides depended on the species examined (GLM, $\chi^2_{[3]} = 11.80$, $P = 0.008$). This effect was driven by a 184% (95% confidence interval (CI): 25%–542%) increase in Bald Eagle abundance and a 91% (95% CI: 12%–227%) increase in Great Blue Heron abundance in the intertidal zone at head of Ladysmith Harbour while the tide was receding compared with while the tide was incoming (Figs. 3*a* and 3*b*, respectively). Abundance of Glaucous-winged Gulls and Northwestern Crows did not clearly differ between receding and incoming tides (Glaucous-winged Gulls estimate (95% CI) = –49% (–158%–16%), Fig. 3*c*; Northwestern Crows estimate (95% CI) = 28% (–140%–296%), Fig. 3*d*). Across the plainfin midshipman breeding season, Glaucous-winged Gull abundance decreased by one individual every 8.75 days (95% CI: 6.58–13.07 days; Fig. 4*c*; GLM, species × day of year interaction, $\chi^2_{[3]} = 33.53$, $P < 0.001$). Additionally, the abundance of the four species at head of Ladysmith Harbour did not clearly vary with low tide height (GLM, $\chi^2_{[1]} = 33.53$, $P = 0.14$). In the Ladysmith Harbour model, day ID accounted for a variance (±SD) of 0.073 ± 0.270 and year accounted for a variance of 0.165 ± 0.407.

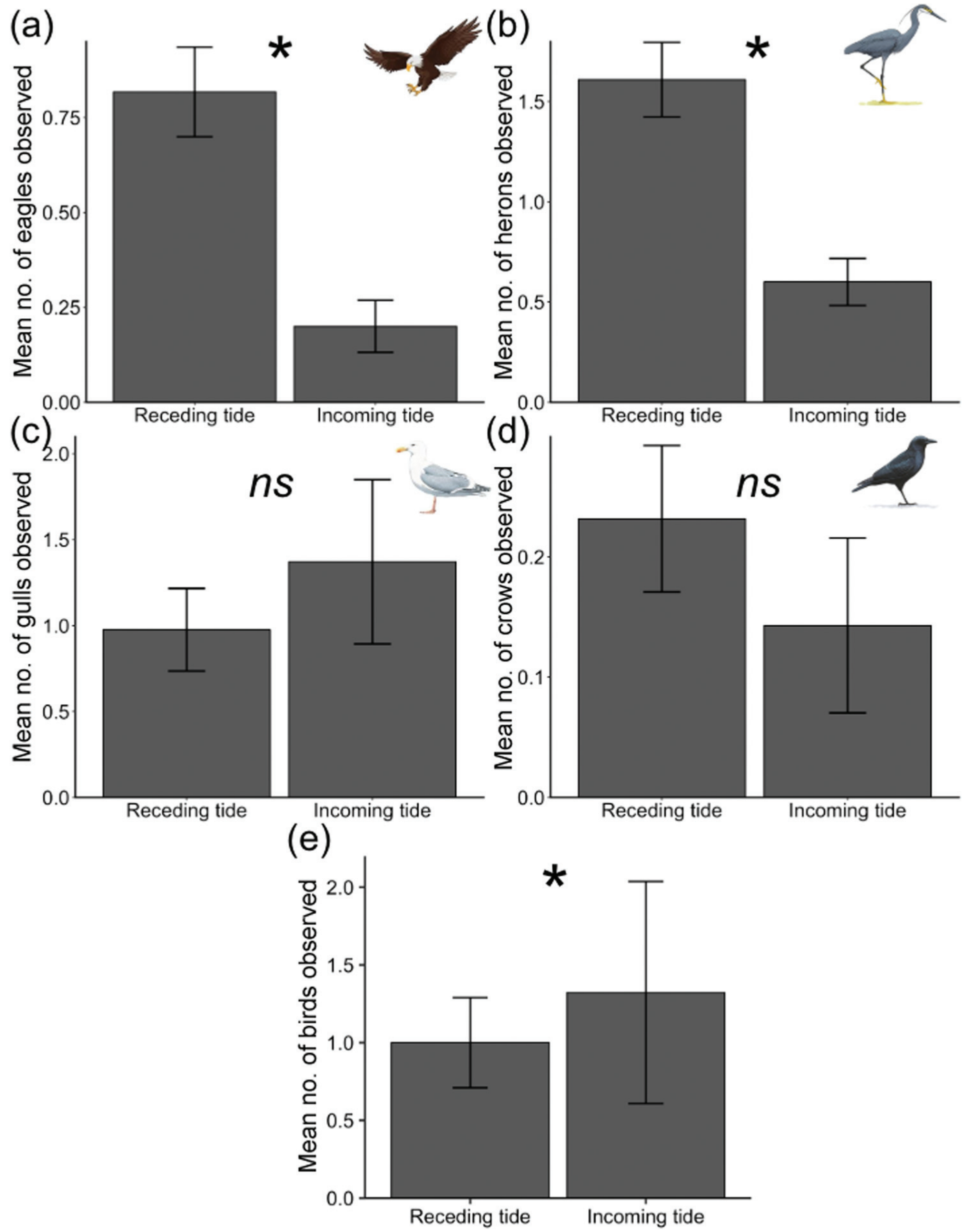
Across our 77 bird censuses at Dabob Bay, we recorded a mean of 1.13 avian predators (median: 0; range: 0–22). On days when at least some plainfin midshipman nests were emersed, avian predator abundance was 239% (95% CI: 38%–733%) higher compared with days when no plainfin midshipman nests were emersed. Furthermore, on days when plainfin midshipman nests were emersed, avian predator abundance increased by 277% (95% CI: 92%–642%) when the tides were incoming compared with when they were receding (Fig. 3*e*). Additionally, total predator abundance decreased by one bird every 18.76 days (95% CI: 11.82–45.66 days) from 23 April to 8 June 2019 (Fig. 4*e*). In the Dabob Bay model, day ID accounted for a variance (±SD) of 1.029 ± 1.014.

Discussion

In this study, we describe how the abundances of four avian predators varied according to the availability of a transiently available intertidal prey fish across three time scales: the diurnal and lunar tidal cycles and the plainfin midshipman breeding season. At a plainfin midshipman breeding site at the head of Ladysmith Harbour where we collected censuses across 6 years, Bald Eagle and Great Blue Heron abundances in the intertidal zone were roughly 3 and 2 times higher, respectively, when the tide was receding compared with when it was incoming. Additionally, we found that the abundance of Glaucous-winged Gulls decreased by one individual every ~9 days over the course of the plainfin midshipman breeding season (21 April to 19 July). In 2019, at a site in Dabob Bay, the combined abundances of all four avian predators was ~2.5 times higher on days when plainfin midshipman nests were exposed by the low tide compared with days when nests were continuously submerged, and total predator abundance decreased by one individual every ~19 days between late April and early June. Our results show that these four avian predators forage in rocky intertidal zones between April and July, predominately on days when at least some plainfin midshipman nests are exposed to the air. Therefore, we suggest that active plainfin midshipman breeding sites provide a time-limited but predictable food source for these birds.

Our predator scans at the head of Ladysmith Inlet suggest that the abundances of Bald Eagles and Great Blue Herons in plainfin midshipman breeding sites are higher when the tide is receding than when it is incoming. This pattern may be explained by several non-mutually exclusive mechanisms related to foraging efficiency. First, plainfin midshipman densities in tide pools and near the shoreline (where Bald Eagles and Great Blue Herons predominantly forage) may be depleted due to foraging by avian predators during the receding tide. Similarly, plainfin midshipman densities may be greater during the receding tide because plainfin midshipman males typically remain close to the water's surface during this period to compete for nests and mates (N.S.B. Houpt, personal observation). Third, foraging efficiency during the incoming tide may be reduced due to increased turbidity resulting from higher levels of suspended sediment swept up by the flood-

Fig. 3. Mean daily abundance of (*a*) Bald Eagles (*Haliaeetus leucocephalus*), (*b*) Great Blue Herons (*Ardea herodias*), (*c*) Glaucous-winged Gulls (*Larus glaucescens*), and (*d*) Northwestern Crows (*Corvus caurinus*) observed during receding and incoming tides at head of Ladysmith Harbour, British Columbia, Canada. (*e*) Mean daily abundance of all avian predators during the receding and incoming tides at Dabob Bay, Washington, USA. Error bars indicate ±1 SE. The asterisk denotes a significant difference at $P < 0.05$. Colour version online.

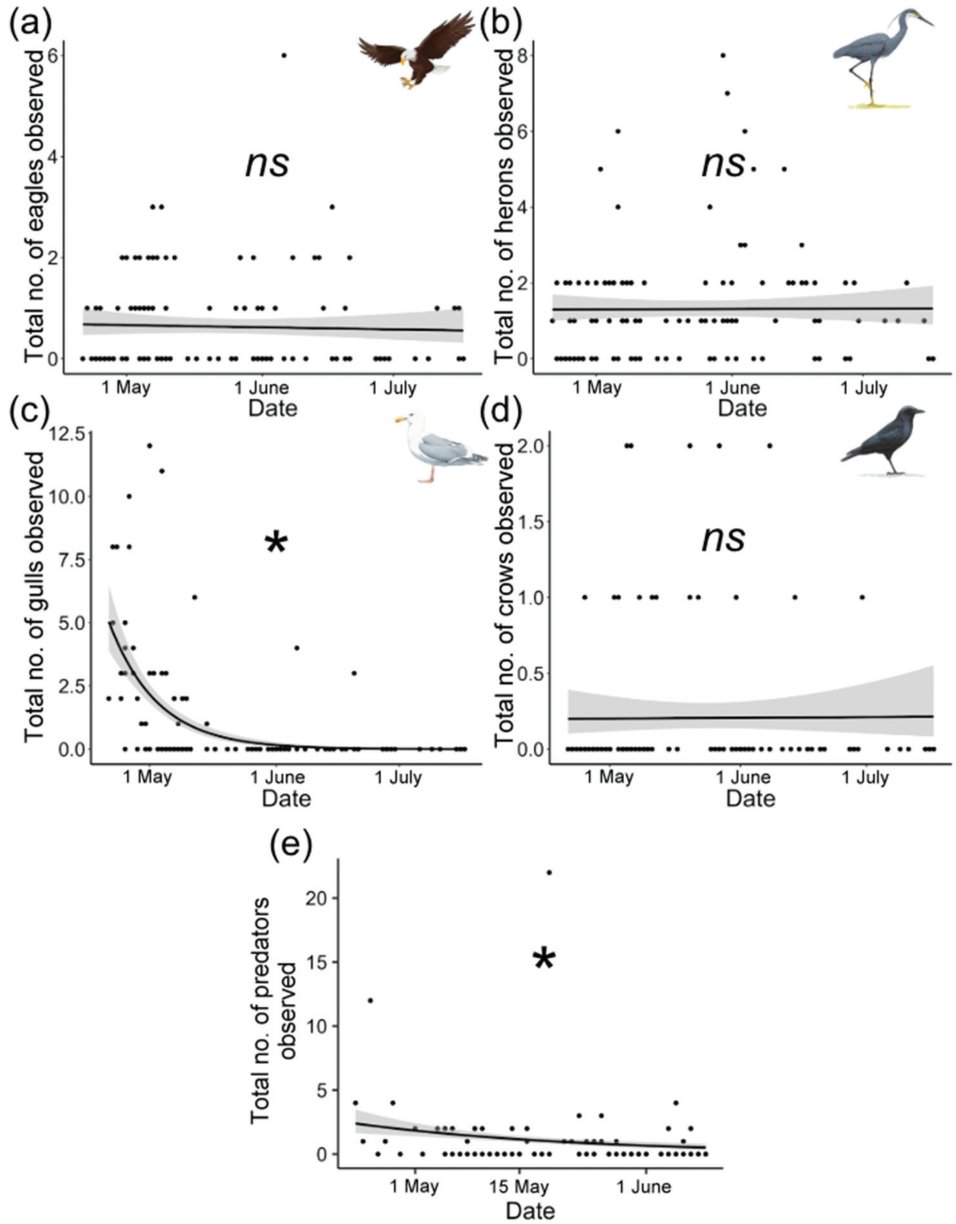


ing water (Postma 1961). In support of our findings, a recent study found a similar temporal pattern of Bald Eagle foraging activity at a rocky intertidal zone in Dabob Bay (Gordon and Bahls 2018). Notably, we had conflicting results at our site in Dabob Bay, where we found that total predator abundance was higher during the incoming tide than during the receding tide, suggesting that the relationship between abundance and tidal stage might be beach-specific. Further research will be required to understand why avian predator abundances are sensitive to particular phases of the diurnal tidal cycle.

Our results showed that the abundance of Glaucous-winged Gulls foraging in intertidal zones at the head of Ladysmith Harbour decreased over the plainfin midshipman breeding season. This pattern is likely the result of gulls migrating to nearby gull colonies as their own breeding season began. Large Glaucous-winged Gull colonies exist on Mandarte Island and Mitlenatch Island, which are 56 and 136 km from Ladysmith Harbour, respectively (Barry 2015). Glaucous-winged Gulls begin to breed on Vancouver Island in late May (Vermeer 1963), which coincides with the steep drop-off in their abundance that we observed at Ladysmith Harbour. In contrast, Bald Eagles, Great Blue Herons, and Northwestern Crows, which did not decrease in abundance over time (Figs. 4*a*, 4*b*, and 4*d*), all initiate breeding near Ladysmith Harbour before the plainfin midshipman breeding season (Vermeer and Morgan 1989, Gebauer and Moul 2001, and Butler et al. 1984, respectively).

Contrary to the other avian predators that usually consumed entire plainfin midshipman carcasses, we observed that Northwestern Crows only partially consumed the fish. Closer inspection of the partially eaten fish carcasses abandoned by Northwestern Crows revealed that they often consumed just the liver and occasionally the ovaries of female fish as well. This surprising behav-

Fig. 4. Total number of (*a*) Bald Eagles (*Haliaeetus leucocephalus*), (*b*) Great Blue Herons (*Ardea herodias*), (*c*) Glaucous-winged Gulls (*Larus glaucescens*), and (*d*) Northwestern Crows (*Corvus caurinus*) observed in relation to day of year at head of Ladysmith Harbour, British Columbia, Canada. (*e*) Abundance of all avian predators at Dabob Bay, Washington, USA, in relation to date. Data visualized in panels *a*–*d* are pooled across 6 years. The 95% confidence interval is indicated by the grey shading. The asterisk denotes a significant difference at $P < 0.05$. Colour version online.



iour could be explained by the marginal value theorem (MVT) (Charnov 1976). MVT predicts that predators will abandon partially consumed prey when the energetic benefits of continuing to forage on the prey are less than the mean energetic benefits of searching for new prey (Sih 1980; e.g., Ernsting and van der Werf 1988; Lykouressis et al. 2016; Lincoln and Quinn 2019). There could be substantial energetic and even survival costs for a small-bodied Northwestern Crow to fully subdue and immobilize a plainfin midshipman and dismember its carcass before consuming. By quickly piercing the soft abdomen of the fish and consuming only the lipid-rich tissues of the liver and ovaries (Muñoz-Cueto et al. 1996), Northwestern Crows might find it more profitable to abandon the remaining carcass and begin searching for new prey items at low tide when the fish are plentiful in the dense breeding grounds of plainfin midshipman.

Plainfin midshipman fish appear to be a significant component of several avian piscivore diets at certain beaches in western North America (Forbes 1982; Elliott et al. 2003; Gordon and Bahls 2018), and the present study suggests that these birds travel to the intertidal zone during low tides to access them. The transfer of nutrients from marine to terrestrial ecosystems through avian predation on plainfin midshipman might constitute an important marine subsidy, which could increase the productivity of nearshore ecosystems (Wipfli et al. 2003; Spiller et al. 2010; Cox et al. 2020). Therefore, protection of plainfin midshipman breeding habitats might contribute to the conservation of avian piscivores and other nearshore species in this region. Plainfin midshipman fish represent a relatively large prey item (up to 30 cm in standard length; Bose et al. 2018) for these birds, they have a long (4 month) breeding season, nest in dense clusters on rocky beaches

(1.21 nests/m² at certain intertidal beaches; Cogliati et al. 2014), and most importantly, are accessible to avian predators at low tide (Gordon and Bahls 2018). Although plainfin midshipman are currently abundant, the global trend of decreasing seagrass habitats (Orth et al. 2006), which are heavily used by juvenile plainfin midshipman (Kelly et al. 2007; Robinson and Yakimishyn 2013), could decrease their recruitment in the coming decades (Heck et al. 2003). If seagrass beds continue to decline (Waycott et al. 2009; Doney et al. 2012), then plainfin midshipman populations might follow, potentially removing an important food source for avian piscivores in the Northeast Pacific. Research on the effects of eelgrass bed destruction on plainfin midshipman reproductive success and, in turn, its cascading effect on bird populations is an important next step in the preservation of the prey-base of these avian species.

In conclusion, this study has provided a first glimpse into the relationship between piscivorous shorebirds, the periodicities of the diurnal and lunar tidal cycles, and the accessibility of the abundant but transiently accessible plainfin midshipman in rocky intertidal zones in western North America. Consumption of these fish by avian predators is likely to be of ecological importance due to the high numbers of plainfin midshipman consumed by shorebirds at certain beaches (Elliott et al. 2003; Gordon and Bahls 2018) and the link this creates between marine and terrestrial ecosystems (Wipfli et al. 2003; Spiller et al. 2010; Cox et al. 2020). Ricketts and Calvin's (1948) classic *Between Pacific Tides*, forwarded by John Steinbeck, presented to its reader details from the lives of intertidal organisms as they compete and coexist with each other in this harsh and dynamic habitat. This text describes how intertidal organisms are influenced by multi-species interactions and the unique ecological constraints imposed by this habitat. Although it is primarily a text on the natural histories of invertebrates, the authors of *Between Pacific Tides* would attest that the intertidal zone provides for a multitude of vertebrates as well, marine and terrestrial alike, whose behaviours and interactions are also intricately linked to the tides, which is the case with the plainfin midshipman fish and their avian predators.

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