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Harlequin Ducks (*Histrionicus histrionicus*) Scavenge Sea Urchin Fragments from Foraging Sea Otters (*Enhydra lutris*)

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Foraging animals may risk association with potential predators to obtain otherwise inaccessible prey. We observed this strategy in wintering Harlequin Ducks (*Histrionicus histrionicus*) scavenging fragments of Red Sea Urchins (*Mesocentrotus franciscanus*) from foraging Sea Otters (*Enhydra lutris*) that were re-occupying an area from which they had been ecologically absent since about 1850. Harlequin Ducks, like other sea ducks, have not previously been reported scavenging from other birds or mammals. In British Columbia, Red Sea Urchins have reached large sizes and densities since the removal of Sea Otter predators by the marine fur trade in the 18th and 19th centuries. Observations of Sea Otters and Harlequin Ducks were made in 4 areas, spanning a time gradient of Sea Otter occupation from 1 to 5 years. During 3 months of observations (December 2013 – February 2014), Harlequin Ducks were associated with foraging Sea Otters only at sites that were recently occupied by Sea Otters (≤ 2 months), where the proportion of urchins in Sea Otter diets was highest and where the ducks acquired urchin fragments from foraging Sea Otters. We suggest that Sea Otters re-occupying their historic range and consuming predominantly large Red Sea Urchins provide a temporarily available prey subsidy for Harlequin Ducks. Our observations document a novel effect of Sea Otters providing important prey supplementation to a marine bird when foraging in urchin-rich habitats, contributing to the overall role of Sea Otters as a keystone species.

Key Words: Sea Otters; *Enhydra lutris*; sea ducks; Harlequin Ducks; *Histrionicus histrionicus*; Red Sea Urchins; *Mesocentrotus franciscanus*; prey subsidies; prey availability; wintering habitat; nearshore ecology; British Columbia

Introduction

Foraging theory predicts that efficiency declines with length of time spent searching for and capturing prey (Stephens and Krebs 1986). Predators can influence the foraging success and strategies of other species by providing access to food items they would otherwise be unable to obtain (Brockman and Barnard 1979). Food stealing and scavenging behaviours are widespread among all taxa, but are particularly prevalent in species with high cognitive ability, such as birds (Morrand-Ferron *et al.* 2007). Low food availability (Oro 1996) or poor foraging technique, for example among juveniles (Skórka and Wójcik 2008), can increase the tendency for an animal to scavenge or steal food from a predator. For example, ravens scavenge at wolf kills in winter when food availability is otherwise low and the birds' energetic demands are greatest (Stahler *et al.* 2002). Diving birds or mammals can attract non-diving or shallow-diving species when they bring deep-dwelling prey items to the surface (Brockman and Barnard 1979); for example, Slender-billed Shearwaters (*Ardenna tenuirostris*) scavenge fish scraps from Steller Sea Lions (*Eumetopias jubatus*) at the surface (Ryder 1957). Such scavenging and food stealing behaviour can increase foraging efficiency (Brockman and Barnard 1979), especially when predators make inaccessible prey items available.

Sea Otters (*Enhydra lutris)* are marine carnivores that regularly dive to depths of 40 m to forage on benthic invertebrates (Riedman and Estes 1990; Bodkin *et al.* 2004; Tinker *et al.* 2008). Sea Otters eat and handle prey at the surface, typically while floating on their back, a behaviour that could make subtidal prey more visible and accessible to shallow or non-diving scavengers. Birds including Bald Eagles (*Haliaeetus leucocephalus*; Watt *et al.* 1995) and gulls (Family Laridae; Fisher 1939) are known to scavenge or steal prey items from Sea Otters. The diets of gulls and eagles differ between areas with and without Sea Otters due to changes – induced by Sea Otters – in the community structure of kelp forest ecosystems (Irons *et al.* 1986; Anthony *et al.* 2008). In Alaska, Sea Otters may directly compete

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with sea duck populations, including eider ducks and scoters by consuming the same benthic invertebrate prey (Terborgh and Estes 2010). Associating with Sea Otters may be high-risk behaviour for some bird species because Sea Otters have occasionally been observed catching and killing waterfowl (Riedman and Estes 1990).

Sea Otters were extirpated from British Columbia in a commercial fur trade that started in the late 1700s (Kenyon 1969). The last known Sea Otter in the province was killed in 1929 (Cowan and Guiguet 1960). From 1969 to 1972, Sea Otters were reintroduced to the west coast of Vancouver Island (Bigg and MacAskie 1978), and since then, have expanded their range along much of the British Columbia coast (Nichol *et al.* 2015). Range expansion in Sea Otters occurs when groups of male otters relocate to the periphery of the range where, in the absence of Sea Otter predation, invertebrate prey have grown large and abundant (Lafferty and Tinker 2014). At newly occupied sites, Sea Otters consume primarily sea urchins, which in British Columbia are the large, Red Sea Urchin (*Mesocentrotus franciscanus*; Breen *et al.* 1982; Ostfeld 1982; Watson and Estes 2011; Honka 2014). Red Sea Urchins are brightly coloured and may be conspicuous to a suite of visual predators, including seabirds and ducks, when brought to the surface by Sea Otters.

Sea ducks are known to be responsive to novel or episodic food sources (Wormington and Leach 1992; Rodway *et al.* 2003; Lacroix *et al.* 2005). However, there are no observations of sea ducks obtaining food by scavenging, although this has been observed in other waterfowl groups (Walter and Becker 1997; Garthe and Hüppop 1998). In British Columbia, Harlequin Ducks (*Histrionicus histrionicus*) winter in nearshore, coastal areas (Iverson *et al.* 2004; Iverson and Esler 2006) and migrate in spring to freshwater streams to breed and nest. During winter, Harlequin Ducks feed intensely to meet the costs associated with maintenance and thermoregulation (Goudie and Ankney 1988) and to attain optimal body mass needed for successful reproduction (Bond and Esler 2006; Esler and Bond 2010). In wintering habitats, Harlequin Ducks eat small intertidal invertebrates, such as snails, crabs, amphipods, and limpets, which they obtain by head-dipping and shallow diving (Vermeer 1983; Gaines and Fitzner 1987; Rodway and Cooke 2002; Bond and Esler 2006; Esler and Bond 2010).

In this paper, we describe our observations of Harlequin Ducks scavenging from Sea Otters. This is the first observation that we know of to document scavenging behaviour in Harlequin Ducks and a commensal association between Harlequin Ducks and a carnivore. We suggest that the opportunity to scavenge food was made possible by Sea Otters re-occupying subtidal rocky habitat in the same area as wintering Harlequin Ducks, and the sudden availability of fragmented Red Sea Urchin prey at the sea surface. We further suggest that, when Sea Otters occupy areas of high sea urchin density, they can provide a temporarily available prey subsidy to Harlequin Ducks.

Study Area

We conducted foraging observations of Sea Otters from December 2013 to February 2014 on the west coast of British Columbia, Canada. We established 4 sites (Figure 1) varying in terms of time since Sea Otter re-occupation from 1 newly established site (as of January 2014) to sites of longer occupation times, ranging from 6 months to 5 years. All sites were located in the nearshore environment. Because of weather conditions and accessibility, most of our observations were conducted at sites occupied for 6 months or less.

Methods

Foraging observations

We used a 50–80× magnification Questar telescope to determine the number, size, and species of prey a Sea Otter collected on each foraging dive (see also Watt *et al.* 2000; Bodkin *et al.* 2001; Dean and Jewett 2001; Tinker *et al.* 2008 for description of the methods). Sea Otters typically forage by diving successively for prey items. Focal animals were observed over a sequence of foraging dives, which is referred to as a foraging bout. We drew or photographed nose scar patterns of focal Sea Otters (Gilkenson *et al.* 2007) to avoid repeated observations of the same individual throughout our study period.

Foraging bouts ranged from 1 to 36 dives. Observations stopped if the Sea Otter stopped foraging, the observer lost sight of the Sea Otter, or after 1 hour of observation of an individual Sea Otter. The proportion of each prey type brought to the surface in each foraging bout was calculated by dividing the number of a specific prey (e.g., Red Sea Urchin) brought to the surface during a foraging bout by the total number of prey items of all types brought to the surface during the bout. For each foraging bout observed, we recorded whether Harlequin Ducks were present (within 1 Sea Otter body length) or absent and, when present, whether they consumed Sea Otter prey scraps (Figure 2). The maximum number of Sea Otters observed at the study site was recorded each day.

Data analysis

Sea Otter occupation time is known to have a negative relation with sea urchin abundance, as Sea Otters remove urchins from the habitat (Estes *et al.* 1982; Ostfeld 1982; Tinker *et al.* 2008; Honka 2014). To explore the effect of Sea Otter occupation time on the number of urchins consumed in Sea Otter diets, we used a non-parametric Kruskal–Wallis test to determine significant differences in the mean proportion of urchin consumed in foraging bouts among sites. We explored occupation time to establish whether the proportion of urchins declined as occupation time increased — as in other studies — and if so, whether we could assume

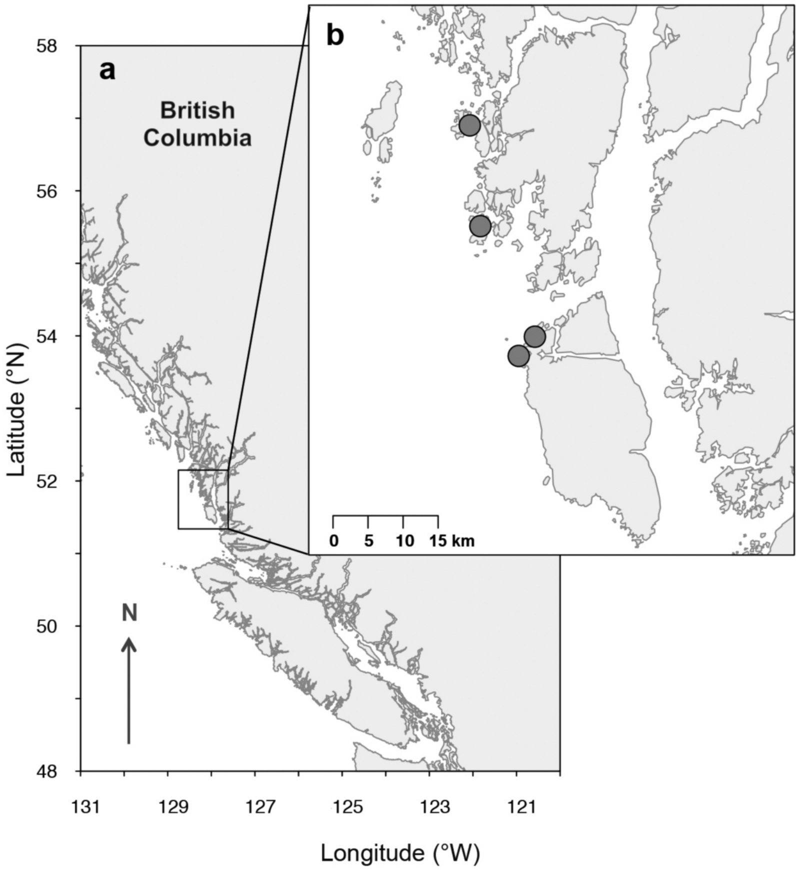

FIGURE 1. The coast of British Columbia (a), and study sites (grey circles in b). From north to south, Sea Otters (*Enhydra lutris*) arrived at these sites in 2009, 2011, January 2014, and July 2013.

FIGURE 2. Sea Otter (*Enhydra lutris*) off the west coast of British Columbia, with Harlequin Duck (*Histrionicus histrionicus*) nearby consuming Red Sea Urchin (*Mesocentrotus franciscanus*) fragments made accessible by the Sea Otter. Photo: Erin Rechsteiner.

that the availability of sea urchin scraps to Harlequin Ducks occurs where urchins are large and abundant, but not when Sea Otters are foraging in locations where urchins are small and few. In this regard, time since Sea Otter occupation was used as a surrogate for the condition of urchin beds rather than an effect in and of itself.

We investigated the importance of both the proportion of sea urchins in the diet and the abundance of Sea Otters in the study area on the scavenging behaviour of Harlequin Ducks. We explored these 2 variables because Harlequin Ducks were only observed interacting with Sea Otters when the otters brought sea urchin prey to the surface (i.e., the ducks ignored the otters when other prey types were brought to the surface) and, where we saw more Sea Otters foraging in an area, there was a concurrent increase in large, brightly coloured sea urchin tests floating at the sea surface, that resulted in an obvious visual cue which may have, in part, attracted the ducks.

Results

We observed 1207 dives in 122 Sea Otter foraging bouts (Table 1). Prey types brought to the surface by foraging Sea Otters were predominantly sea urchins, turban snails, clams, and crabs, and Sea Otter diets differed among sites (Figure 3). The mean proportion of sea urchins in Sea Otter diets differed significantly among sites ($\chi^2 = 52.72$, $P < 0.001$) and was highest at sites recently colonized by Sea Otters, where urchins were presumably abundant (Figure 3).

Although Harlequin Ducks were present at all four sites, they were only observed scavenging Sea Otter prey fragments at Choked Pass, where the proportion of Red Sea Urchin in the diet was highest (0.68). When Harlequin Ducks were present at other Sea Otter sites, they did not interact with the otters. At Choked Pass, Harlequin Ducks scavenged from Sea Otters in 16% of foraging bouts. The number of ducks present during a foraging bout ranged from 1 to 10 (mean 1.9, standard error 0.32, $n = 12$). Harlequin Ducks were only observed to interact with Sea Otters when they brought sea urchins to the surface and the ducks did not scavenge any other prey types.

We found evidence that both the proportion of Red Sea Urchins brought to the surface and the number of Sea Otters counted at the foraging sites may be important in predicting the scavenging behaviour of the Harlequin Ducks (Figure 4). Harlequin Ducks were more often present when the proportion of sea urchin in an individual Sea Otter's foraging bout was high (median 0.88; Figure 4) and were more often present when the number of Sea Otters in the study area was high (median 63; Figure 4).

Discussion

In this study, we observed overwintering Harlequin Ducks scavenging on scraps of Red Sea Urchin generated by foraging Sea Otters. Our observations suggest that a high abundance of Sea Otters with a high proportion of Red Sea Urchin in their diets provide an opportunity for opportunistic scavenging by Harlequin Ducks. Harlequin Ducks only scavenged urchin scraps and did not interact with Sea Otters consuming other prey types. From our observations, Red Sea Urchins, being large and brightly coloured, provided obvious visual cues. We could typically spot a Red Sea Urchin at the sea surface immediately before our focal Sea Otter resurfaced, whereas other prey items of Sea Otters were rarely as large or as brightly coloured. Because Harlequin Ducks are visual predators, we suspect the ease of observing sea urchin prey would have attracted the ducks to high densities of foraging otters that were focused on urchins. Harlequin Ducks were most often present on foraging bouts where otters brought up a majority of Red Sea Urchins on successive dives (median 0.88 proportion urchin in a foraging bout) and ducks were typically absent on dives where the proportion of urchin was lower (median 0.23 proportion urchin in a foraging bout). Our observations suggest that Sea Otters re-occupying historic habitat where Red Sea Urchins are large and plentiful provide an important, but temporary, prey subsidy to Harlequin Ducks.

As Sea Otters expand into new habitat they forage on large and abundant prey, usually sea urchins (Estes and Palmisano 1974; Breen *et al.* 1982; Ostfeld 1982; Laidre and Jameson 2006; Tinker *et al.* 2008; Watson and Estes 2011; Honka 2014). Range expansion often

TABLE 1. Level of foraging activity by Sea Otters (*Enhydra lutris*) observed at each study site on the west coast of British Columbia from December 2013 to February 2014.

Site	Occupation time, years	No. dives	No. bouts	Dives/bout, mean ± SE	No. otters, mean ± SE
Choked Pass	0.17	727	77	9.4 ± 0.9	64 ± 4.7
West Beach	0.5	226	21	10.8 ± 1.8	49 ± 8.6
Breadner Group	3	136	13	10.5 ± 2.0	17 ± 0*
Simonds Group	5	118	11	10.7 ± 3.1	40 ± 0†

*Two days of observation were conducted at this site; the Sea Otter count was the same on both days.
†One day of observation was conducted at this site.
Note: SE = standard error.

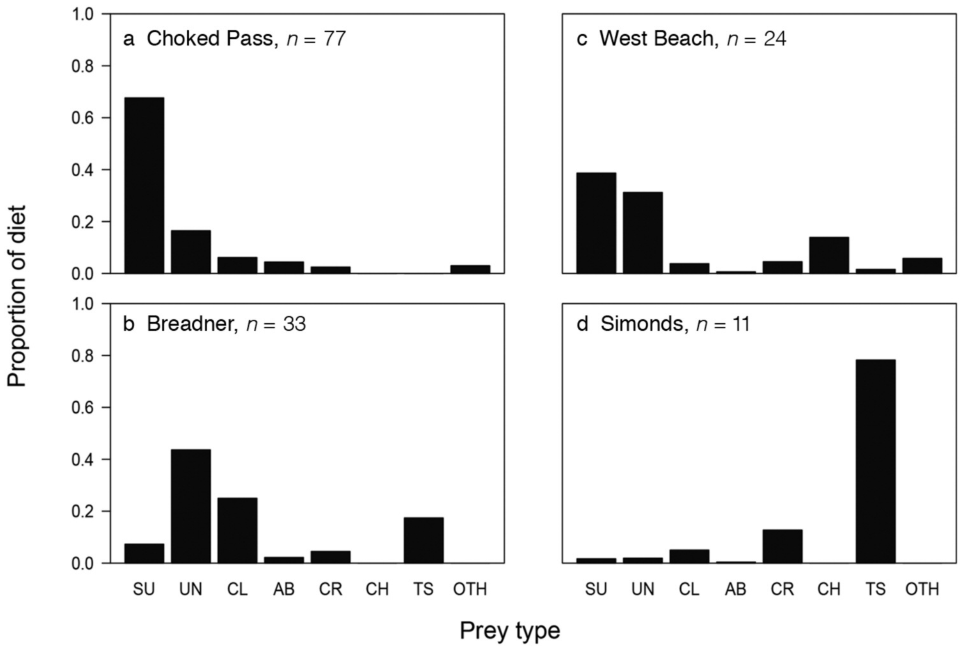

FIGURE 3. The proportion of prey types brought to the surface during Sea Otter (*Enhydra lutris*) foraging bouts (n) observed at our 4 study sites. Note: SU = sea urchin, UN = unidentified, CL = clam, AB = abalone, CR = crab, CH = chiton, TS = turban snail, OTH = other prey type.

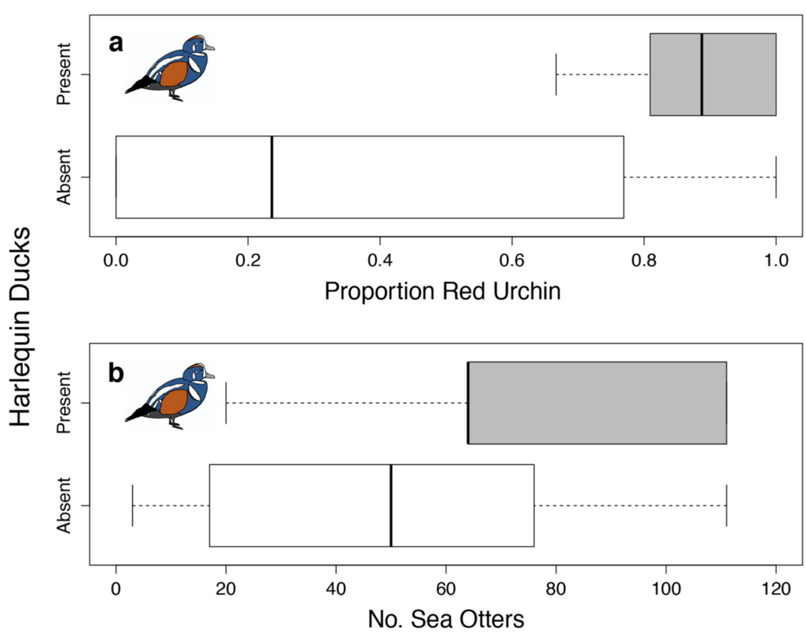

FIGURE 4. Presence and absence of Harlequin Ducks (*Histrionicus histrionicus*) related to (a) the proportion of Red Sea Urchin (*Mesocentrotus franciscanus*) in the foraging bout and (b) the number of Sea Otters (*Enhydra lutris*) in the foraging area. Dark vertical lines indicate the median, box edges indicate the 1st and 3rd quartiles, and dashed lines indicate the range. Illustration: Angeleen Olson.

occurs during the winter when rafts of non-territorial male Sea Otters leave food-limited areas to exploit large and abundant prey at the periphery of the range (Jameson 1989; Lafferty and Tinker 2014). This can result in peripheral groups of male Sea Otters eating and fragmenting large red urchins where Harlequin Ducks are also wintering.

Although Sea Otters and Harlequin Ducks both forage in exposed, nearshore habitats for at least several months of the year, to the best of our knowledge, they have not previously been observed interacting (J. A. Estes, personal communication, 2014; D. Esler, personal communication, 2015). The interaction between Sea Otters and Harlequin Ducks may have been previously overlooked because observations require recent recolonization by otters and winter feeding observations of both Sea Otters and Harlequin Ducks. The effect of returning Sea Otters on Harlequin Ducks illuminates another way that Sea Otters make for more robust species assemblages via both direct and indirect effects.

Harlequin Ducks typically forage on intertidal snails, crabs, amphipods, and limpets (Vermeer 1983; Gaines and Fitzner 1987; Rodway and Cooke 2002; Bond and Esler 2006; Esler and Bond 2010) in waters less than 5 m deep (Holm and Burger 2002), whereas Red Sea Urchins occur in the shallow subtidal area to depths up to 125 m (McCauley and Carey 1967), and are rare in Harlequin Duck diets. Urchin size can affect their quality as prey, with large reproductive urchins being higher in lipids and key nutrients than the smaller immature individuals that might be available to Harlequin Ducks unassisted by Sea Otters (Oftedal *et al.* 2007). Of the sea urchins consumed by Sea Otters at Choked Pass, 87% had a test diameter equal to or larger than about 7.5 cm, and Harlequin Ducks not scavenging on otter prey typically consume invertebrates that are less than 2 cm in diameter (Vermeer 1983). The Red Sea Urchins brought to the surface by Sea Otters would have been too large and collected at depths too deep for Harlequin Ducks to either handle or dive for. The role of Sea Otters in fragmenting the urchin prey to sizes that could be handled by ducks likely drove the commensal interaction that we observed.

Wintering male and female Harlequin Ducks store nutrients and lipids in preparation for spring migration and breeding, aiming for an optimal premigration weight (Bond and Esler 2006; Esler and Bond 2010). Bond and Esler (2006) found that Harlequin Ducks that fed on herring roe at wintering sites spent less time foraging but gained weight more rapidly than ducks that did not eat herring roe. The ability to acquire energy rapidly at wintering sites by adapting foraging strategies to exploit new prey items may benefit Harlequin Ducks when they return to their nesting sites in spring.

Although the effects of Sea Otters on kelp forest ecosystems are well known, our observations reveal another pathway by which otters induce direct effects on the nearshore environment, contributing to their overall role as keystone predators. Sea Otters provided a useful dietary supplement to a sea bird that may be energetically constrained during winter (Goudie and Ankney 1986; Esler *et al.* 2002) and for which winter survival has the potential to be a demographically limiting stage in the annual cycle (Esler *et al.* 2000). This is also the first observation that we know of, of Harlequin Ducks scavenging from a carnivore, illuminating the plasticity in foraging strategies that these ducks can employ. Our observations suggest that Sea Otter range expansion and the associated sea urchin consumption in recently colonized areas provides a temporarily available prey resource for Harlequin Ducks that may increase their fitness in the short term during a period of Sea Otter population recovery.

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