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Choosing among mobile prey species: Why do gulls prefer a rare subtidal crab over a highly abundant intertidal one?

Julie C. Ellis [a,*], Katherine E. Allen [b], Michelle S. Rome [b], Myra J. Shulman [c]

[a] Department of Environmental and Population Health, Tufts University Cummings School of Veterinary Medicine, 200 Westboro Rd., North Grafton, MA 01536, USA
[b] Shoals Marine Laboratory, Cornell University, Ithaca, NY 14853, USA
[c] Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA

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ABSTRACT

In New England, Herring Gulls (*Larus argentatus*) and Great Black-backed Gulls (*L. marinus*) are generalist predators that forage on highly mobile prey in intertidal and shallow subtidal zones, including three species of crabs: *Cancer borealis*, *C. irroratus*, and *Carcinus maenas*. *Carcinus* is more abundant than are *C. irroratus* and *C. borealis* and yet both *Cancer* species are more common in the diet of gulls. In this study we used a series of experiments to examine why gulls exhibit disproportionately higher predation on *C. borealis* relative to the two other crab species. We found that gulls do not discriminate among crab species when presented crab tissue "patties" indicating that gulls do not select crabs based on differences in palatability. At smaller size ranges (<75 mm carapace width), *C. irroratus* had lower dry tissue weight than the other two species, thus gulls should prefer similar-sized *C. borealis* and *Carcinus* based on their caloric value. At carapace widths greater than 80 mm, *C. irroratus* had higher available dry tissue weight than *C. borealis*. However, *C. borealis* is generally larger than *C. irroratus* in the intertidal and shallow subtidal zones so this difference is unlikely to contribute to a preference for *C. irroratus*. Our experiments showed that algal species dominating rocky ledges provide a cryptic refuge for *Carcinus* thereby reducing the likelihood of attack by gulls. We found that the "lateral merus" display exhibited by *C. irroratus* appears to deter attacks by gulls; in contrast, *C. borealis* withdraw their chelae in response to attack, which likely facilitates their capture by gulls. During simulated gull attacks, *Carcinus* exhibited escape behavior whereas *C. borealis* remained stationary. Lack of escape behavior likely facilitates capture of *C. borealis* by gulls. In sum, our findings suggest that gulls have formed a search image for *C. borealis*, which is likely a result of the relative ease of capture and profitability of *C. borealis* compared to *Carcinus* and *C. irroratus*. Gull preference for *C. borealis* has important consequences for crab distributions and the structure of rocky intertidal and shallow subtidal zones in New England. In particular, gulls create a refuge for *Carcinus* in the intertidal zone by reducing densities of *C. borealis*, a potential predator and competitor, and by avoiding preying upon *Carcinus*.

1. Introduction

Predation can have strong ecological effects, influencing population sizes, community composition, and species diversity. However, the impact of predators depends on their prey choices. Selection of dominant versus inferior competitors, or abundant versus rare species, can greatly alter the magnitude of a predator's impact on the ecological community. Predators also exert strong selection on prey populations, with subsequent evolution of prey defenses that in turn may alter the choices made by future generations of predators. Thus, understanding how predators choose among multiple prey species contributes to a greater understanding of selection pressures on prey and the influence of predators on communities.

In coastal New England, Herring Gulls (*Larus argentatus* Pontoppidan, 1763) and Great Black-backed Gulls (*L. marinus* Linnaeus, 1758) are generalist predators that regularly forage on highly mobile intertidal and subtidal prey (Ellis et al., 2007; Good, 1992). Included in the diet are three species of crabs: *Cancer borealis* (Stimpson, 1859), *C. irroratus* (Say, 1817), and *Carcinus maenas* (Linnaeus, 1758) (henceforth referred to as *Carcinus*). Predation by gulls results in the virtual exclusion of *C. borealis* from the low-mid intertidal zone and produces a trophic cascade through enhancement of snail (*Littorina littorea*) and mussel (*Mytilus edulis*) populations (Ellis et al., 2007). Gull predation on *C. borealis* also results in increased populations of two other mesopredators, *Carcinus* and the carnivorous snail, *Nucella lapillus*. Interestingly, gulls consume *C. borealis* at disproportionately high rates relative to its abundance in the intertidal and shallow subtidal zones (Ellis et al., 2005; Rome and Ellis, 2004). Most strikingly, *Carcinus* is far more abundant than are *C. irroratus* and *C. borealis* (Donahue et al., 2009) and yet both *Cancer* species are much more common in the diet of gulls (Ellis et al., 2005).

* Corresponding author. Tel.: +1 508 887 4933; fax: +1 508 839 7946.
E-mail address: julie.ellis@tufts.edu (J.C. Ellis).

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Prey may suffer disproportionately higher rates of predation due to a variety of reasons: differences in profitability (calories/handling-time), abundance, palatability, digestibility, search time (including effects of prey crypticity), escape behaviors and defensive capabilities. There is an extensive literature documenting prey behavior and decision making under predation risk, but predator foraging decisions in relation to prey characteristics have been less well studied (Lima, 2002; Shultz and Finlayson, 2010) but, see (Van Gils et al., 2005). Numerous studies suggest that foraging predators select prey based on their encounter frequency or relative abundance; searching predators should show biases toward the most abundant prey types (Pulliam, 1974; Sherratt and Harvey, 1993; Yearsley, 2003). Much of the evidence supporting frequency-dependent selection by predators comes from foraging experiments using passive or immobile prey; however, predator choice has been shown to be very different when predators feed on mobile prey (Sih and Christensen, 2001). That is, encounter rates for mobile prey are not simply a function of prey densities, but instead are modified by mobility as well as crypticity. The majority of studies that examine prey selection by predators in rocky intertidal zones have focused on sessile or slow-moving prey including limpets, sea urchins, mussels, sea stars, snails, sea anemones, and chitons (Donahue et al., 2009; Irons et al., 1986; Lopez et al., 2010; Silva et al., 2010; Snellen et al., 2007; Yoshiyama et al., 1996). Prey mobility and defensive behaviors are likely to affect prey selection, but studies are lacking for intertidal and shallow subtidal predators of such prey.

In this study we first determine gull prey preferences when different crab species are equally available and unable to use escape or defense behaviors. We then address the question of why gulls exhibit disproportionately higher predation on *Cancer* spp. relative to *Carcinus*, and on *C. borealis* relative to *C. irroratus*, and the related question of how gulls distinguish among crab species. We consider a number of hypotheses and perspectives: (1) Palatability may differ among the crab species; (2) Crabs of the same size but different species may vary in tissue mass available to gulls; (3) Differences in coloration (crypticity) or shape among crab species may affect the likelihood of predation by gulls; (4) Behavioral defenses by the crabs may influence gull prey selection; and/or (5) Escape responses may differ among the crab species and affect the likelihood of successful predation by gulls.

2. Methods

2.1. Study site and species

The study was conducted at the Shoals Marine Laboratory, Appledore Island, in the Gulf of Maine (42 58′N; 70 37′W). Appledore Island is part of a nine island archipelago located 10 km east of the coast of New Hampshire. The eastern side of the island is exposed to heavy wave action from the Atlantic Ocean, whereas the western side is relatively protected. The shoreline is dominated by rock ledges and boulder coves.

In the Gulf of Maine, Herring Gulls and Great Black-backed Gulls forage in the rocky intertidal and shallow subtidal zones (Ellis et al., 2007), mainland landfills, the open ocean, and behind fishing boats (Good, 1998; Pierotti and Good, 1994). Gulls capture prey in shallow subtidal areas by paddling on or flying close to the water, then plunging to a maximum depth of 1 m below the water surface (Good, 1998). Gulls also forage in the intertidal zone during low tide by walking along the shoreline and capturing prey from within the algal canopy or from rock crevices. The rocky intertidal zone where gulls forage can be divided into three distinct zones characterized by the predominant sessile species: the barnacle zone (2.1 – 2.7 m above mean lower low water [MLLW]), the *Ascophyllum* (*A. nodosum*) zone (0.6 – 2.1 m), and the *Chondrus* (*C. crispus*) zone (0.6 m to shallow subtidal). Gulls primarily feed in the *Chondrus* and *Ascophyllum* intertidal zones, as well as the shallow subtidal zone adjacent to the shore (Ellis et al., 2005; Rome and Ellis, 2004).

Gulls capture crabs during ebbing tides, typically while paddling on the surface of the water and plunge diving. Gulls sometimes swallow small crabs whole, but gulls grab most crabs by a leg or claw and transport them to shore where they are dismembered prior to consumption. After dropping the crab on the shore, the gull flips the crab over on its dorsal side, rips off the legs and claws, pierces the ventral carapace, and then consumes the muscles and organs contained within the dorsal carapace.

The three crab species on which gulls forage are (in order of increasing body and chela size): *Carcinus maenas* (family Portunidae), *Cancer irroratus* and *C. borealis* (family Cancridae) (Fig. 1). All three species share trophic and spatial resources and have morphological characteristics typical of predatory decapods, including large chelate first thoracic appendages (Jeffries, 1966). *Carcinus* and *C. irroratus* are generally fast moving and highly active on open substrates (Elner, 1981; Jeffries, 1966; Moody and Steneck, 1993). In contrast, *C. borealis* are slower but have stronger chelae (Jeffries, 1966; Moody and Steneck, 1993). Both *C. irroratus* and *Carcinus* respond to threats by either fleeing or performing a stereotypical lateral merus display during which the crabs raise and extend their chelipeds (Novak, 2004; Richards, 1992). In contrast, *C. borealis* crouches down rather than fleeing and folds its appendages to cover its mouthparts and ventral surface (Novak, 2004; Richards, 1992). The two crab genera are quite different in coloration. *Carcinus* has a dark green exoskeleton, which matches the color of dominant algae in the low- and mid- rocky intertidal zones of New England. In contrast, the two *Cancer* species have pink exoskeletons, which match the coralline algae that often cover the rocky substrate in sea urchin barrens (Dumas and Witman, 1993). Though the two *Cancer* species are very similar in color and general shape, subtle differences include a much smoother carapace texture for *C. irroratus*, and larger, coarser carapace teeth for *C. borealis*.

2.2. Palatability of different crab species

One possible explanation for the disproportionate rates of predation is that the 3 crab species differ in palatability. To test this hypothesis, we constructed an experiment to determine whether gulls showed any preferences among crab tissue when all visual cues as to species identity had been removed, and no prey defenses were present. We dissected individuals of each of the three species of crabs and removed all internal meat and organs, which were then crushed and homogenized. The homogenized tissue was placed into a circular mold (3.5 cm diameter × 2.5 cm in height) and frozen into crab patties. In each experimental trial, we placed three crab patties (one per species) in a line within the territory of a gull pair, and recorded which patty was eaten first and whether all three patties were eaten. Each trial was conducted in a different gull territory and the spatial ordering of crab patties was randomized for every trial. A total of 36 trials (18 per gull species) were conducted in gull breeding colonies on Appledore Island.

2.3. Differences in tissue mass among crab species

Gulls may select among crab species based upon differences in available calories provided by otherwise similar-sized crabs. To determine whether this might explain the different rates of predation on the 3 crab species, we examined the relationship between crab size (carapace width) and the dry mass of the tissues consumed by the gulls. Here we explicitly assume that the proportion of dry tissue mass that is digestible by the gulls is similar among the three species of crabs. We collected 20–40 individuals of each crab species from intertidal and shallow-subtidal areas around Appledore Island. These crabs represented the range of sizes encountered by foraging gulls (Rome and Ellis, 2004). Maximum carapace width was measured and then the soft tissue in the carapace (muscles, stomach, gonads, gills, cartilage, and other organs/tissues) was dissected from each crab. Muscle tissues in the legs