BEHAVIORAL ECOLOGY - ORIGINAL PAPER

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A tra t The distribution of predators is widely recognized to be intimately linked to the distribution of their prey. Foraging theory suggests that predators will modify their behaviors, including movements, to optimize net energy intake when faced with variation in prey attributes or abundance. While many studies have documented changes in movement patterns of animals in response to temporal changes in food, very few have contrasted movements of a single predator species naturally occurring in dramatically di

addressing the behavioral and functional relationships between predators and their prey, which in turn have direct implications for conservation and management of species and their habitats.

Ideal free distribution (IFD) concepts predict that predator densities should be positively correlated with prey densities (Fretwell and Lucas 1970). Similarly, foraging theory suggests that animals behave in ways that optimize energy intake (Stephens and Krebs 1986). Accordingly, changes in the distribution of predators resulting from movements by individuals can reXect the underlying diVerences in the availability or quality of prey within a habitat. Prey attributes also dictate how much space a predator must use to meet its energetic requirements (i.e., its home range, McNab 1963; Harestad and Bunnel 1979). Habitats with high resource availability allow individuals to meet daily and seasonal requirements within relatively small areas (Fisher 2000; Smith and Schaefer 2002). However, if there is temporal or spatial variability in resource availability, then individuals must modify their behavior. One important implication of this environmentally mediated response by predators is modiWcation of distributions and movements as individuals shift to occupy more proWtable foraging areas when prey availability declines (Charnov et al. 1976; Pyke 1983; Stephens and Krebs 1986). Patchy spatial distribution, ephemeral availability, and rapid depletion by conspeciWcs have all been shown to lead to increased movement probability and larger home ranges for predators (Tufto et al. 1996; Ferguson et al. 1999).

Along with habitat and prey features, sex and age can inXuence movements, site Wdelity, and dispersal (Greenwood 1980). Male-biased movement is common, as males often range farther in mate-searching activities (Greenwood 1980; Rohwer and Anderson 1988; Robertson and Cooke 1999). For example, pair bonding occurs in late winter for many waterfowl including sea ducks (Robertson and Cooke 1999), and unpaired males searching for females could show longer distance movements and increased overall space use. Juveniles often demonstrate increased movement and lower site Wdelity (Baldassarre et al. 1988; Robertson and Cooke 1999; Cooke et al. 2000), potentially because they are unfamiliar with wintering areas or they may be excluded from optimal habitats by more dominant adult foragers.

Numerous empirical studies have described the movement responses of animals to temporal changes in prey distribution, abundance, or quality (Van Eerden 1984; Einarsson 1988; Tufto et al. 1996; Warnock and Takekawa 1996; MarzluV et al. 1997; Ferguson et al. 1999). However, few studies have had the data to evaluate the movement behavior of a single species in dissimilar foraging landscapes using multiple data sources. We evaluate movements, home range size, site Wdelity, and distributional

consistency of a molluscivorous sea duck, the surf scoter (   ), which winters in two distinct habitats on the PaciWc coast of North America: soft-bottomed intertidal Xats where clams are the primary prey and rocky intertidal shores where mussel

or internal coelomic VHF transmitters with external anten-nae were implanted following procedures described by Mulcahy and Esler (1999). Implanted transmitters have been shown to perform well for scoters, with low mortality eVects and good signal strength and accuracy (Iverson et al. 2006

would die in the interval between detections i and $i + 1$ with the probability it would leave the foraging site where it began the winter period (Bennetts et al. 2001, Iverson and Esler 2006). An encounter history was created for each bird based on 1-week intervals beginning in early December and ending in early March. During each interval, individuals were listed as faithful (stayed within its original foraging site, or a directly adjacent site, during that interval), moved (located in a new site during the interval), temporarily censored (undetected in that interval, but later located), or permanently censored (dead, failed radio, or had moved in a previous interval). Our dataset included 128 individuals with valid encounter histories (Baynes Sound $n = 59$; Malaspina Inlet $n = 69$) and employed a logit link to bound parameter estimates and ensure numeric optimization (Cooch and White 2006). A total of ten models were included in our candidate set, with study area, sex, age, a fully parameterized model of study area + sex + age, and a null model each incorporated with and without time dependency (week). By considering only single variable models of our three primary parameters of interest (study area, sex, and age), we reduced the possibility of Type I errors associ-

total number of surf scoters was also more constant than in mussel foraging sites. A recent study in Baynes Sound showed that scoters there are not constrained by amount of daylight (i.e., they do not forage nocturnally, Lewis et al. 2005) nor by prey availability, as foraging eVort did not increase as clams were depleted (Lewis et al. 2008). Together, these data corroborate the conclusion that Baynes Sound is a highly stable winter habitat for scoters.

The signiWcant depletion of mussels in Malaspina Inlet indicates that this area is a high quality habitat that is heavily used by ducks. When prey densities are suYciently high, i.e., early in winter, mussel habitats may be very proWtable, due to the reduction or elimination of dive, search and handling times. The mussels available on Malaspina Inlet shellWsh aquaculture structures were not only abundant and visible, but occurred on Xoating or very shallow structures, reducing foraging costs relative to dives required to search for clams (De Leeuw 1996). The energetic costs of diving may be an especially important constraint for ducks in winter, already facing high thermo-regulation costs and daylight limitations. Mussels are generally swallowed underwater and require no surface handling time (De Leeuw 1999), while larger prey such as clams have a capture success rate of only 50% (Lewis et al. 2008) and may require signiWcant surface handling time, thus increasing time investment in each prey capture (Guillemette et al. 1992). Foraging on mussels also allows scoters to minimize shell intake. The shell minimization

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