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DO WINTERING HARLEQUIN DUCKS FORAGE NOCTURNALLY AT HIGH LATITUDES?

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Abstract. We monitored radio-tagged Harlequin Ducks (*Histrionicus histrionicus*) to determine whether nocturnal feeding was part of their foraging strategy during winter in south-central Alaska. Despite attributes of our study site (low ambient temperatures, harsh weather, short day length) and study species (small body size, high daytime foraging rates) that would be expected to favor nocturnal foraging, we found no evidence of nocturnal dive-feeding. Signals from eight radio-tagged Harlequin Ducks never exhibited signal loss due to diving during a total of 780 minutes of nocturnal monitoring. In contrast, the same eight birds exhibited signal loss during 62 ± 7% (SE) of 5-minute diurnal monitoring periods (total of 365 minutes of monitoring). Our results suggest that Harlequin Ducks in south-central Alaska face a stringent time constraint on daytime foraging during midwinter. Harlequin Ducks wintering at high latitudes, therefore, may be particularly sensitive to factors that increase foraging requirements or decrease foraging efficiency.

Key words: Alaska, Harlequin Duck, Histrionicus histrionicus, *nocturnal foraging, radio telemetry, time constraint, winter.*

¿Acaso el Pato *Histrionicus histrionicus* Forrajea Durante la Noche a Altas Latitudes?

Resumen. En este estudio monitoreamos patos *Histrionicus histrionicus* marcados con radio transmisores para determinar si la alimentación nocturna es parte de su estrategia de forrajeo durante el invierno en el sur-centro de Alaska. A pesar de que se esperaría que el forrajeo nocturno fuera favorecido por las características de nuestro sitio de estudio (temperaturas ambientales bajas, clima inclemente, días de corta duración) y de la especie estudiada (tamaño corporal pequeño, altas tasas de forrajeo durante el día), no encontramos evidencia de alimentación mediante buceo en la noche. Las señales emitidas por los transmisores acoplados a ocho individuos nunca se redujeron como consecuencia de actividades de buceo durante un total de 780 minutos de monitoreo nocturno. En contraste, los mismos ocho individuos evidenciaron pérdidas de la señal durante el 62% ± 7% (EE) de los períodos de monitoreo diurnos de cinco minutos de duración (en total se monitorearon 365 minutos). Nuestros resultados sugieren que los patos *H. histrionicus* están sujetos a una fuerte limitante de tiempo en cuanto al forrajeo diurno durante el invierno medio en el sur-centro de Alaska. Por lo tanto, los individuos que pasan el invierno en latitudes altas podrían ser particularmente sensibles a factores que incrementen los requerimientos de forrajeo o que disminuyan la eficiencia de forrajeo.

Foraging behavior can be adjusted in response to changing conditions to optimize energy intake (Schoener 1971, Pyke 1977). Thus foraging behavior is fundamentally linked to fitness because energy intake has direct effects on survival. Birds have been shown to increase their foraging activity in association with increased maintenance energy costs or decreased food availability (Owen et al. 1992, Percival and Evans 1997, McKnight 1998, Webster and Weathers 2000, Cope 2003). Some species that normally feed only during daylight extend foraging into the nocturnal period in response to reduced day length (Systad et al. 2000, Systad and Bustnes 2001), or disturbance during diurnal foraging time (Thornburg 1973, Lane and Hassel 1996). Sea ducks (Anatidae: Mergini) are generally believed to be visual foragers that are limited by light conditions to forage only during daylight (Owen 1990, McNeil et al. 1992), although few data exist to support this assumption (Guillemette 1998). However, recent studies of sea ducks wintering at high latitudes have found that some species feed during darkness when day length is short (Systad et al. 2000, Systad and Bustnes 2001).

Requirements for energetically efficient foraging in Harlequin Ducks (*Histrionicus histrionicus*) are likely highest during mid-winter when harsh environmental conditions increase maintenance energy requirements, and short day length decreases time available for diurnal foraging (Goudie and Ankney 1986). Among sea ducks, Harlequin Ducks are small-bodied (0.4–0.8 kg), and hence have higher mass-specific metabolic rates, higher rates of heat loss, and are less able to rely on

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stored reserves for extended periods (Calder 1974). Indeed, foraging accounts for >70% of Harlequin Duck diurnal activity in the winter, and time spent foraging has been found to be negatively correlated with temperature and day length (Goudie and Ankney 1986, Fischer and Griffin 2000). Given the high proportion of the day spent feeding, Harlequin Ducks face a stringent time constraint on increasing diurnal foraging (Goudie and Ankney 1986). Nocturnal foraging, however, could ease the constraint of short day length for Harlequin Ducks wintering at high latitudes by extending foraging beyond the diurnal period.

We examined the nocturnal behavior of Harlequin Ducks wintering in Resurrection Bay, on the south-central coast of Alaska, near the northern limit of their winter range (Robertson and Goudie 1999). Using radio telemetry, we looked for evidence of dive-feeding at night during the winter of 2001–2002. Our objective was to better understand the winter foraging ecology of Harlequin Ducks and to directly test the assumption that this species is constrained to forage during daylight. Also, Harlequin Ducks are considered to be particularly sensitive to changes in their wintering environment and have been shown to respond more strongly than other species to anthropogenic disturbance (Esler et al. 2002). Therefore, the results of this study are relevant for evaluating whether Harlequin Ducks can employ nocturnal foraging to accommodate anthropogenic disturbance and other factors affecting foraging efficiency on the wintering grounds.

METHODS

This study was conducted in Resurrection Bay (60°6′N, 149°24′W), a glacial fjord located on the southeast side of the Kenai Peninsula, Alaska. Harlequin Ducks were captured at Lowell Point, an alluvial fan on the west side of the bay 3 km south of the town of Seward. The shoreline immediately north and south of Lowell Point slopes steeply into subtidal habitat, while the point is gently sloping with a large expanse of intertidal habitat composed of boulder, cobble, and gravel sediment. Maximum tide level range in Resurrection Bay is 5 m during winter. A group of ca. 35 Harlequin Ducks wintered along Lowell Point in 2001–2002.

On 13 and 14 October 2001 we captured Harlequin Ducks using a modified floating mist net (Kaiser et al. 1995). Ten Harlequin Ducks, six males and four females, were captured and surgically implanted with radio-transmitters (Holohill Systems Ltd., Ontario, Canada). Radio-transmitters weighed 18.8 g (<3% of adult body mass), had a 6-month battery life expectancy, a pulse rate of 44–46 pulses per minute, and a mortality switch that doubled the pulse rate if the transmitter remained motionless for ≥12 hr. Surgeries to implant radio-transmitters were conducted at the Alaska SeaLife Center in Seward, Alaska by a veterinarian experienced with the procedure and under protocols approved by the Institutional Animal Care and Use Committee of the Alaska SeaLife Center (protocol 00–005). Surgically implanted transmitters have been used successfully in previous studies with Harlequin Ducks and were found to carry a low risk of mortality (Mulcahy and Esler 1999). Radio-tagged birds were held for one hour after surgery and then released at the location of their capture.

Radio signals were monitored from a remote-telemetry station consisting of two mast-mounted, four element Yagi antennas connected to an Advanced Telemetry System R4000 receiver (Isanti, Minnesota) located on the hillside above the capture location at an elevation of ca. 70 m. Loss of radio-signal reception was used as an indicator of diving behavior (Custer et al. 1996, Jodice and Collopy 1999). Daytime visual observations of radio-tagged birds confirmed that pulses were inaudible during dives and audible again upon resurfacing. During each remote-signal monitoring session, the radio frequency from each radio-tagged bird was monitored for signal reception loss caused by diving behavior during a period of 5 minutes. Radio-tagged birds not detected were recorded as absent from the study area. We conducted radio-signal monitoring sessions during both diurnal and nocturnal periods; we defined the diurnal period as ranging from 30 minutes before sunrise until 30 minutes after sunset. Radio signals were monitored at least once per week from November 2001 through March 2002.

Because not all radio-tagged birds were detected during each signal monitoring session, detection rates during diurnal and nocturnal signal monitoring sessions were calculated for each radio-tagged bird as the percentage of signal monitoring sessions during which each bird was present in the study area. Diurnal and nocturnal detection rates were averaged across all radio-tagged birds. For each radio-tagged bird, the percentage of 5-minute signal monitoring periods during which the bird was detected in the study area and its signal was lost due to diving was calculated and averaged across all birds for diurnal and nocturnal sessions as estimates of diving frequency during day and night. Estimates are presented as mean ± SE.

RESULTS

Of the 10 Harlequin Ducks radio-tagged, one individual was never detected after release. The radio signal from a second individual was not heard until seven weeks after release when its mortality signal was detected and its freshly killed carcass was found in a tree commonly used by Bald Eagles (*Haliaeetus leucocephalus*). Because these two birds were never detected in the study area alive, they did not contribute any signal monitoring data. The remaining eight radio-tagged birds were detected alive and in the study area during the study period.

Signals from radio-tagged Harlequin Ducks were monitored during a total of 34 sessions between November 2001 and March 2002: 22 sessions at night and 12 sessions during the day. Signal monitoring sessions were distributed throughout both the diurnal and nocturnal periods and were conducted across a broad range of tide levels and weather conditions. Most radio-tagged birds were detected during each signal monitoring session, although the average number of birds detected during nocturnal sessions (7.0 ± 0.2, n = 22 sessions) was slightly greater than the average number detected during diurnal sessions (6.2 ± 0.3, n = 12 sessions). The average detection rate for radio-tagged birds during nocturnal signal monitoring ses-

TABLE 1. Number of signal detections for each of eight radio-tagged Harlequin Ducks, and number of detections during which diving behavior was indicated by signal loss for diurnal (n = 12 sessions) and nocturnal (n = 22 sessions) periods during winter 2001–2002 in Resurrection Bay, Alaska.

Radio frequency	Diurnal period		Nocturnal period	
	Detections	Detections with diving	Detections	Detections with diving
6.903	3	1	17	0
7.032	8	6	20	0
7.056	12	9	20	0
7.207	12	9	21	0
7.221	12	9	18	0
7.245	3	1	19	0
7.307	12	7	20	0
7.320	11	8	21	0
Mean ± SE	9.1 ± 1.4	6.2 ± 1.2	19.5 ± 0.5	0.0 ± 0.0

sion was 89 ± 2% (an average of 19.5 detections during 22 nocturnal monitoring sessions) and was less variable than the average detection rate during diurnal signal monitoring sessions (76 ± 10%, or an average of 9.1 detections during 12 diurnal monitoring sessions; Table 1). Signal loss indicative of diving was not heard from any radio-tagged Harlequin Duck during a total of 780 minutes of nocturnal monitoring. In contrast, signal loss indicative of diving was heard during an average 62 ± 7% of diurnal detections of birds present in the study area (a total of 365 minutes of signal monitoring; Table 1). Thus diving behavior was never detected at night but was detected frequently during the day.

DISCUSSION

We found no evidence that radio-tagged Harlequin Ducks wintering in Resurrection Bay foraged by diving at night. High nocturnal detection rates and absence of signal loss indicative of diving behavior are consistent with the hypothesis that Harlequin Ducks rest in groups offshore at night (Fischer and Griffin 2000, Rodway and Cooke 2001). The more variable average detection rate during the day compared to night, and the high percentage of daytime detections with signal loss due to diving may reflect higher levels of activity and movements to feeding areas out of detection range.

Despite challenging ambient temperature (mean −4.4°C, range −23.9°C to 6.1°C; NOAA 2002) and photoperiod (mean 8.3 hours, range 6.8 to 11.4 hours; U. S. Navy 2002) conditions during our study period, we did not detect nocturnal dive-feeding by Harlequin Ducks. The apparent absence of nocturnal dive-feeding behavior in the Harlequin Ducks monitored in this study may indicate that dive-feeding is not energetically profitable at night. Nilsson (1970) speculated that sessile prey may be more available to dive-feeding waterfowl at night than motile prey. King Eiders (*Somateria spectabilis*) and Common Eiders (*S. mollissima*), both large species of sea ducks that feed on sessile invertebrates by diving, responded to reduced photoperiod and harsh weather conditions at a 70°N latitude wintering site by foraging during early morning and late evening darkness, suggesting that these species were able to forage profitably under low light conditions (Systad et al. 2000).

Relatively sessile prey (e.g., snails, limpets, chitons, mussels), however, compose only a portion of the winter diet of Harlequin Ducks (Vermeer 1983, Goudie and Ankney 1986, Gains and Fitzner 1987, Fischer and Griffin 2000). If motile prey (e.g., amphipods, isopods) are unavailable to Harlequin Ducks at night, the overall density of prey available to nocturnally foraging birds would be reduced relative to prey densities encountered during the day. In addition, sessile prey have lower energy content than motile prey (Goudie and Ankney 1986, Fischer and Griffin 2000). Given that diving is an energetically expensive behavior (Lovvorn and Jones 1991), and capture success would likely be reduced by decreased prey density and decreased prey conspicuousness at night (Schoener 1971), the costs associated with nocturnal dive-feeding likely outweigh the potential benefits.

Some species of waterfowl may forage profitably at night by foraging in areas with high densities of prey, or by increasing the efficiency of their foraging behavior. For example, Systad and Bustnes (2001) found that Steller's Eider (*Polysticta stelleri*) wintering at high latitude (70° N) forage at night during midwinter and likely decreased foraging costs by increasing their use of non diving foraging behaviors (surface-feeding, upending) and concentrating foraging activity during low tide. The use of dense kelp beds as foraging habitat, which contain high densities of invertebrate prey (Bustnes and Systad 2001), may increase their foraging efficiency and make feeding at night profitable. Similarly, species of dive-feeding waterfowl wintering in areas with high densities of food often forage at night (Nilsson 1970, Custer et al. 1996).

We found no evidence of nocturnal foraging in Harlequin Ducks, even during low tide levels when diving is most energetically efficient (Systad and Bustnes 2001). Harlequin Ducks occupy rocky, nearshore habitats during winter (Goudie and Ankney 1988, Esler, Bowman et al. 2000). We observed Harlequin Ducks foraging during the day in shallow intertidal habitat using non-diving behaviors; however, non-dive foraging was always observed in association with dive-feeding. We attempted to locate radio-tagged individuals in this study at night on their diurnal foraging area using a handheld receiver and antenna, and found that low signal strength suggested birds were not near shore. We also observed daily offshore movements shortly after sunset by Harlequin Ducks at Lowell Point, as have been documented at other wintering areas (Fischer and Griffin 2000, Rodway and Cooke 2001). Offshore movements by Harlequin Ducks in winter have been hypothesized to be associated with increased predation risk from nocturnally active predators (e.g., mink [*Mustela vison*], Rodway and Cooke 2001). In addition to risk of predation, we speculate that reduced foraging efficiency at night in rocky nearshore habitats may make nocturnal foraging more energetically costly than resting for Harlequin Ducks.

In winter, Harlequin Ducks maintain very high diurnal foraging rates to meet daily energy requirements and may minimize energy expenditure at night by resting, when foraging conditions are likely poor. This hypothesis is supported by increased foraging rates during the evening by wintering Harlequin Ducks that suggests preparation for a period of nonfeeding during the night (Goudie and Ankney 1986, Fischer and Griffin 2000, Heath et al. 2005). The apparent absence of nocturnal dive-feeding in this study, in addition to offshore movements at night, suggest that Harlequin Ducks in south-central Alaska do not feed at night during winter. On northern wintering grounds, reduced day length may place constraints on the amount of time available for diurnal foraging by Harlequin Ducks.

Esler, Schmutz et al. (2000) found that Harlequin Duck survival was reduced in areas affected by the *Exxon Valdez* oil spill compared to unoiled areas, and speculated that subtle changes in energy or time-activity budgets may have caused these differences in survival. Harlequin Ducks appear sensitive to changes in their environment and our finding that Harlequin Ducks wintering in south-central Alaska rarely, if ever, feed at night suggests that they are likely unable to use nocturnal foraging to compensate for anthropogenic alterations (including oil contamination) of their wintering habitat.

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