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 6 SE	9.1 6 1.4	6.2 6 1.2	19.5 6 0.5	0.0 6 0.0

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 ($n \ 5 \ 12 \ sessions$) and nocturnal ($n \ 5 \ 22 \ sessions$) periods during winter 2001–2002 in Resurrection Bay, Alaska.

sion was 89 6 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 6 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 6 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 24.48C, range 223.98C to 6.18C; 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 708N 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 decg8ese

- KAISER, G. W., A. E. DEROCHER, S. GRAWFORD, M. J. GILL, AND I. A. MANLEY. 1995. A capture technique for Marbled Murrelets in coastal inlets. Journal of Field Ornithology 66:321–333.
- LANE, S. J., AND M. HASSAL. 1996. Nocturnal feeding by Dark-bellied Brent Geese *Branta bernicla*. Ibis 138:291–297.
- LOVVORN, J. R., AND D. R. JONES. 1991. Effects of body size, body fat, and change in pressure with depth on buoyancy and costs of diving in ducks (*Aythya* spp.) Canadian Journal of Zoology 69: 2879–2887.
- MCKNIGHT, S. K. 1998. Effects of food abundance and environmental parameters on foraging behavior of Gadwalls and American Coots in winter. Canadian Journal of Zoology 76:1993–1998.
- MCNEIL, R., P. DRAPEAU, AND J. D. GOSS-CUSTARD. 1992. The occurrence and adaptive significance of nocturnal habits in waterfowl. Biological Reviews 67:381–419.
- MULCAHY, D. M., AND D. ESLER. 1999. Surgical and immediate post-release mortality of Harlequin Ducks implanted with abdominal radio transmitters with percutaneous antennae. Journal of Zoo and Wildlife Medicine 30:397–401.
- NILSSON, L. 1970. Food-seeking activity of south Swedish diving ducks in the non-breeding season. Oikos 21:145–154.
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION [ONLINE]. 2002. National Climatic Data Center. , http://www.ncdc.noaa.gov/oa/ncdc.html. (17 November 2004).
- OWEN, M. 1990. Nocturnal feeding in waterfowl. Acta XXth Congressus Internationalis Ornithologici 2: 1105–1112.
- OWEN, M., R. L. WELLS, AND J. M. BLACK. 1992. Energy budgets of wintering Barnacle Geese: the effects of declining food resources. Ornis Scandinavica 23:451–458.
- PERCIVAL, S. M., AND P. R. EVANS. 1997. Brent Geese Branta bernicla and Zostera: factors affecting the

exploitation of a seasonally declining food source. Ibis 139:121–128.

- PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology 52:137–154.
- ROBERTSON, G. J., AND R. I. GOUDIE. 1999. Harlequin Duck (*Histrionicus histrionicus*). In A. Poole and F. Gill [EDS.], The birds of North America, No. 446. The Birds of North America, Inc., Philadelphia, PA.
- RODWAY, M. S., AND F. COOKE. 2001. Effect of food availability on arrivandi.2 Tm 0 Tc A Tm c A Tm a8 0 TD iTr-36