SHORT COMMUNICATIONS

BEHAVIORAL CORRELATES OF HEART RATES OF FREE-LIVING GREATER WHITE-FRONTED GEESE[1]

CRAIG R. ELY, DAVID H. WARD AND KAREN S. BOLLINGER

Alaska Biological Science Center, U.S. Geological Survey, 1011 E. Tudor Road, Anchorage, Alaska 99503,
e-mail: craig_ely@usgs.gov

Abstract. We simultaneously monitored the heart rate and behavior of nine free-living Greater White-fronted Geese (*Anser albifrons*) on their wintering grounds in northern California. Heart rates of wild geese were monitored via abdominally-implanted radio transmitters with electrodes that received electrical impulses of the heart and emitted a radio signal with each ventricular contraction. Post-operative birds appeared to behave normally, readily rejoining flocks and flying up to 15 km daily from night-time roost sites to feed in surrounding agricultural fields. Heart rates varied significantly among individuals and among behaviors, and ranged from less than 100 beats per minute (BPM) during resting, to over 400 BPM during flight. Heart rates varied from 80 to 140 BPM during non-strenuous activities such as walking, feeding, and maintenance activities, to about 180 BPM when birds became alert, and over 400 BPM when birds were startled, even if they did not take flight. Postflight heart rate recovery time averaged < 10 sec. During agonistic encounters, heart rate exceeded 400 BPM; heart rates during social interactions were not predictable solely from postures, as heart rates were context-dependent, and were highest in initial encounters among individuals. Instantaneous measures of physiological parameters, such as heart rate, are often better indicators of the degree of response to external stimuli than visual observations and can be used to improve estimates of energy expenditure based solely on activity data.

Key words: activity, aggression, Anser albifrons, behavior, flight, Greater White-fronted Geese, heart rate.

Heart rate is a good indicator of an animal's energy expenditure (Wooley and Owen 1977, Woakes and Butler 1983), and response to adverse stimuli (Harms et al. 1997) and conspecifics (Kanwisher et al. 1978). The rate at which an animal's heart beats depends not only on physical activity and condition, but also on the level of external stimulation, including both real and perceived threats to its immediate survival and social position. Understanding how heart rate varies with ac-

tivity and social behavior should enable us to better measure energy costs and evolutionary consequences of specific actions and behaviors (Bartholomew 1987).

Heart rate, however, has rarely been measured on wild free-living birds, and the few studies to date (Kanwisher et al. 1978) have monitored very few individuals, or relied on potentially obtrusive, externally-mounted, heart-rate monitors. Heart rates have been published for only one species of goose, the Barnacle Goose, *Branta leucopsis* (Butler and Woakes 1980, Nolet et al. 1992), and these studies were of captive, human-imprinted birds. Here we present the first information on instantaneous heart rates of wild-caught, free-flying waterfowl in known activities. This also is one of the few studies (Kanwisher et al. 1978) to provide information on heart rates of birds conditioned for, and participating in, normal day-to-day activities.

METHODS

We used rocket nets to capture geese on their primary wintering area in the Central Valley of California in December 1996. Ten adult female geese were selected for implants. We studied Tule Greater White-fronted Geese (*A. a. gambeli*) which are somewhat larger than the other subspecies (*A. a. frontalis*) wintering in California (Ely and Dzubin 1994). Transmitters (model HRT-150, Telonics Inc., Mesa, Arizona) were covered in a braided surgical mesh (Marlex Mesh, Davol, Charlotte, North Carolina) and abdominally implanted into the right air sac using standard surgical procedures (Korschgen et al. 1996). Positive and negative leads of the transmitter were placed just beneath the sternum, close to the heart (Butler and Woakes 1979). Each transmitter was secured with sutures placed through the mesh so that the antenna portion of the 44 g radio package was situated on the dorsal side of the abdominal cavity to increase transmission range. Leads were anchored by a single suture at the base of the sternum. Transmitters had a maximum rate of 600 beats min^{-1} and a life expectancy of 4–5 months. Geese were released 2 days after capture.

One of the purposes of the project was to determine the influence of aircraft overflights on the behavior of the geese during summer in Alaska, so radios were programmed to transmit for 15 days after capture in December, and then resume transmission when geese arrived in Alaska in mid April. Hence, we collected

data on heart rates and behavior over the two-week period immediately after release. Birds were observed from a motor vehicle while they were at foraging sites, flying, and at roost sites. Heart rate signals were received with either a 3- or 4-element Yagi antenna held by hand, or mounted in a dual peak/null array on a vehicle. Heart rate signals were fed from a telemetry receiver to a portable tape recorder for later analysis (Kanwisher et al. 1978). Initially, we synchronized observation data with tape recordings by recording precise start times on tapes and in field notes; later, we recorded bird behavior and heart rate simultaneously onto the same audio tape. Heart rates were generally recorded continuously for 1–5 min per bird, during which time the behavior of the focal bird was noted, as well as the behavior of the entire flock. Tape speed was periodically monitored by recording segments with a stopwatch and then timing playback speed. It proved difficult to keep track of flying birds; in instances when an individual could not be followed in flight, we recorded flock behavior.

Observations of behavior were made with 10× binoculars or a 10–60× power spotting scope. We also noted time of day, flock size, presence of other goose species, and habitat in which birds were encountered. Behaviors were assigned to one of seven categories: (1) feed (head down while stationary or moving), (2) rest (neck coiled on back and bill on chest, or head and neck on back with bill pointing towards tail), (3) standing (head up, not moving, but neck bent—as opposed to alert), (4) alert (head up, not moving, neck extended, but back horizontal to ground), (5) alarm (head up, neck fully extended, with chest higher than tail; Lazarus 1978), (6) walk (head up, walking), (7) preen (manipulating feathers with bill), (8) fly (bird in the air and not landing), and (9) landing (bird descending to the ground).

We made digital sound "bytes" of each heart rate recording by playing back tapes of heart rate signals into a sound card on a MacIntosh 7100 computer (Apple Computer Co., Cupertino, California). Heart rates were determined by using an acoustical software package (Canary, Cornell Ornithology Laboratory, Ithaca, New York) that created a spectrogram of heart beats and observer recording relative to a time scale. We determined heart rate from the number of pulses in each 10-sec byte, unless the recording was of a bird in flight, when we used 5-sec bytes to improve resolution for examining characteristics of rapid pulse variations. We also created detailed (<5 sec) heart rate profiles to better characterize responses during periods of rapidly changing heart rates before and after flight, and during aggressive encounters (Figs. 1, 2). Filtering techniques allowed use of recordings with poor signal-to-noise ratios. Occasionally the signal-to-noise ratio was too poor to visually detect all heart pulses on the spectrograms; in most of these instances we could hear the audio signal on playback, and after slowing the playback speed were able to edit the output accordingly.

Patterns of double electrical pulses were occasionally detected in post-operative geese. We verified the nature of electrical impulses and hence origin of paired signals by obtaining electrocardiograms of a restrained bird with a transmitter in place. Paired pulses were determined to be artifactual rather than true multiple contraction events. Occasional irregular pulses are commonly associated with implanted heart rate recorders in birds (C. Harms, pers. comm.); in our birds, such pulses were found to be associated with thoracic muscular contractions. Multiple electrical discharges were almost always detectable, as they were distinctly spaced and tightly grouped. In rare instances when multiple pulses were suspected in the read-out but spacing was not obvious, the heart rate sample was discarded.

Each of the sound bytes from a given behavioral state and time period were pooled into a single bout record. Multiple bouts of the same individual were then used to establish a mean heart rate of each bird in a given activity. Analysis of variance (ANOVA; SAS Institute 1989) was used to detect differences in heart rate among individuals and among behaviors. Significant ANOVAs were followed by LSD multiple comparisons (SAS Institute 1989). To test for individual variation in heart rate, we developed heart rate scores for each bird by ranking each individual within an activity, and calculated ranks based on deviations from mean rankings. Values presented are mean ± standard error (SE).

RESULTS

There was significant variation in heart rate among behaviors ($F_{8,105} = 226.6$, $P < 0.001$; Table 1). Birds engaged in energetically-costly activities such as flying had the highest heart rates. During predator surveillance (alert and alarm), heart rates also were significantly elevated. We detected no significant differences in heart rate among birds in maintenance and foraging activities including walking, feeding, resting, preening, or standing (casual head-up; Table 1). The nonsignificant slower heart rates of walking and feeding geese were likely due to the low heart rate of a single individual (see below).

Heart rates varied significantly among individuals ($F_{8,105} = 2.4$, $P < 0.05$; Table 1), even after we reduced the number of behaviors and individuals in the analysis to minimize number of missing cells in the two-way ANOVA. One bird in particular, number 5675, had substantially lower heart rates than most other individuals when engaged in less taxing activities such as walking, feeding, preening, and casual head-up behavior (Table 1). However, there was significant interaction among behaviors and individuals ($F_{31,105} = 2.0$, $P < 0.01$), as evidenced again by bird number 5675, whose heart rate was amongst the lowest for most activities, but was one of the highest during flight (Table 1). Individual variation in heart rate was not in general related to body mass ($r^2 = 0.01$; $P > 0.5$, $n = 9$; mean of rank score in each behavior relative to body mass), although heavier birds had higher heart rates during flight ($r^2 = 0.50$, $P < 0.05$, $n = 8$).

Heart rates were generally (4 of 5 instances) elevated ($\bar{x} = 176 \pm 87$ beats min^{-1}; BPM) during head shake preflight behavior (Johnsgard 1965). Heart rates of flying birds averaged 413 BPM. This value includes all birds known to be in the air, except those descending to land. Variation in heart rates within and among flying individuals was undoubtedly due in part to var-

TABLE 1. Mean (± SE) heart rates (beats min⁻¹) of Greater White-fronted Geese engaged in different behaviors.[a]

Bird Id.	Body mass (g)	Behavior								
		Walk	Feed	Preen	Rest	Standing	Alert	Alarm	Fly	Landing
5495	2,408	130 ± 5	138	141 ± 6		144	180	180 ± 60	412 ± 14	276 ± 24
5509	2,474	117		126 ± 27		120 ± 11	180	180		
5615	2,416	112 ± 4	108 ± 1	114 ± 3	84	101 ± 6	155 ± 11		370 ± 26	
5625	2,421			103	112 ± 4	133 ± 14		180	447 ± 8	226 ± 10
5645	2,365								437 ± 9	263 ± 20
5675	2,769	73 ± 2	74 ± 1	79 ± 12		71 ± 4	150	180 ± 30	438 ± 13	
5705	2,783			137	118 ± 9				404 ± 23	
5715	2,616	98		95 ± 4		131 ± 35		270	377 ± 24	
5725	2,683			116		114		256	416 ± 7	324 ± 24
Mean ± SE[b]	2,548 ± 55	98 ± 7	98 ± 9	118 ± 5	110 ± 7	114 ± 8	164 ± 8	201 ± 19	413 ± 6	272 ± 15
Among behavior comparisons[c]		E	E	E	E	E	D	C	A	B

[a] Values for each individual are the mean of 1–12 different recordings per behavior ($\bar{x}$ = 17.2 ± 2.3 observations/individual). Values without a SE are of a single observation.
[b] Pooled mean includes all samples from each individual.
[c] Behaviors sharing a common letter are not significantly different.

iable flight characteristics, for which we often could not account.

In several instances, we were able to continuously monitor heart rate and behavior of birds during take-off and landing (Fig. 1). Heart rate was highest during take-off (pumping flight), and lowest when birds were gliding. The mean heart rate of three birds immediately after landing was 229 ± 70 BPM. Recovery of heart rate to normal (non-flight) level was very rapid, requiring < 10 sec in the two instances in which the entire landing sequence was recorded.

On one occasion, we were able to monitor heart rate of a bird throughout an aggressive encounter at a feeding site (Fig. 2). Heart rate increased to 400 BPM in the initial encounter (A; Fig. 2). The bird remained in a threat posture after the initial encounter (B), during which time heart rate lowered briefly to 200 BPM before quickly rising during a joint threat with other family members (C). Heart rate quickly fell when foraging resumed.

DISCUSSION

Lack of variation in heart rate for birds engaged in common field behaviors (walking, foraging, preening, standing) also has been reported for Black Ducks (*Anas rubripes;* Wooley and Owen 1978), and supports the findings of other studies that found little variation in energy expenditure among such activities (Weathers et al. 1984). This is in contrast to some studies (Frederick and Klaas 1982) that have used multiples of basal metabolic rate (Paynter 1974) to build energetic models based on time budget data. In some circumstances, however, it seems that foraging can be an especially costly energetic activity for geese, particularly when excavating subterranean plant parts (Burton et al. 1979). This was not the situation in our study, when geese fed in harvested rice fields on readily available waste grain (C. Ely, unpubl. data).

Individual variation in heart rate has been documented previously in other species of waterfowl (Wooley and Owen 1978, Nolet et al. 1992). Nolet et al. (1992) reported individual variation in daily energy expenditure and heart rate in Barnacle Geese, in a study in which oxygen consumption was measured to calculate the relationship between heart rate and energy expenditure. They also found, as have others (Gessaman 1980), that the relationship between heart rate and oxygen consumption varies among individuals, and emphasized the need to incorporate individual variation in studies of energetics. Despite the prevalence of individual variation, Nolet et al. (1992) concluded that heart rate can be used to estimate energy expenditure in free-living birds. However, the existence of individual variation does necessitate obtaining larger samples to adequately represent population means. Within-population variation in energy expenditure also indicates that differences in body condition (e.g., Ely and Raveling 1989) may not be due solely to variation in foraging abilities and social constraints, but also to basic differences in metabolic rate.

Heart rates of white-fronts in non-strenuous activities (including resting; Table 1) were generally higher than 66–104 BPM as reported for resting Barnacle Geese (Nolet et al. 1992) but lower than 110–240
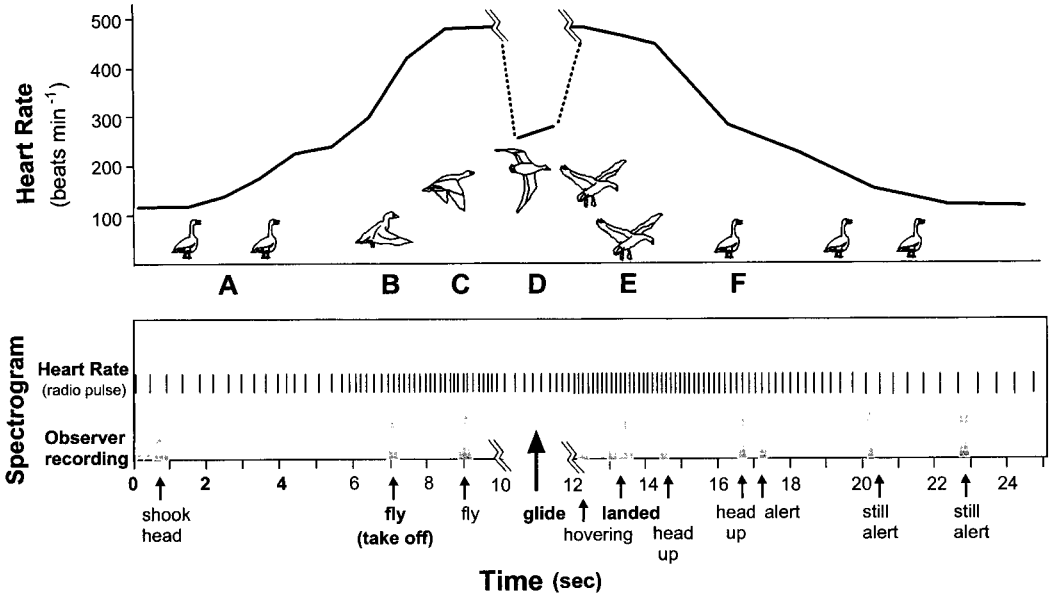
FIGURE 1.   Changes in heart rate of Greater White-fronted Geese recorded during (A) preflight, (B) take-off, (C) flapping flight, (D) gliding, (E) landing, and (F) recovery. Figure is a composite of three different recordings (A–C, D, E–F).
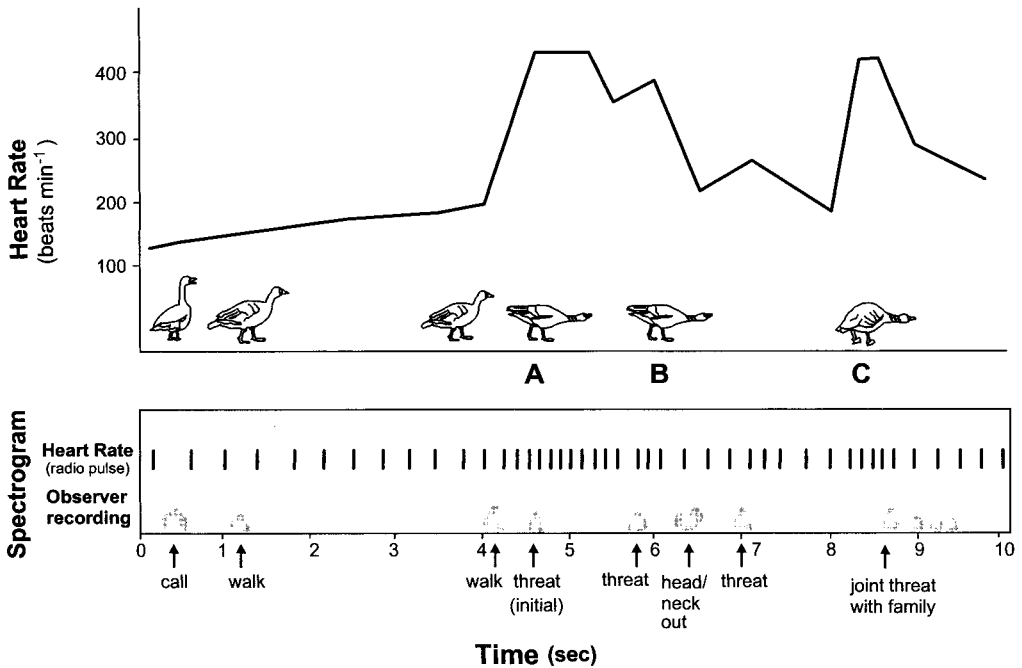

FIGURE 2.   Changes in heart rate of a Greater White-fronted Goose during an agonistic encounter, illustrating (A) rapid increase in heart rate during an initial encounter with a conspecific, and less prolonged responses during (B) a subsequent encounter with the same individual, and (C) during a joint threat with family members.

BPM reported for geese walking at minimum recorded speeds (0.3 m sec^{-1}). However, the studies are not directly comparable, as the lowest heart rates of Barnacle Geese were recorded for quiescent birds that were resting and fasting. Also, the Barnacle Geese were roughly 30% lighter than the 2,550 g geese we studied, and were captive, and likely not as physiologically well conditioned as the wild geese in our study. Heart rates of homeotherms are largely a function of body size (Nagy 1987) and conditioning (Butler and Turner 1988).

Head shaking is a pre-flight behavior in geese that is thought to help maintain family integrity by synchronizing take-off of family members (Raveling 1969). Our findings of increased heart rate during pre-flight activity indicates that head shaking also may serve to physiologically prepare birds for strenuous activity.

Variation in heart rate of white-fronts during hovering, gliding, and flapping flight supports findings for other species of birds (Butler 1991). Wind speed and direction also influence the cost of flight. Flying into a wind will normally increase the cost of flight, but the air flow over the wing will minimize the energy expended and heart rate observed during landing, when heart rates are similar to birds gliding or slope soaring (Fig. 1). Butler and Woakes (1980) reported a heart rate of 261 BPM in slope soaring Barnacle Geese.

The potential energy cost of aggression and other social behaviors has frequently been alluded to, but there have been few direct or indirect (Kanwisher et al. 1978) measures of energy expenditure during such activities. Studies that have related energy expenditure to social behavior have relied generally on captive or semi-captive animals (Walsberg 1983, Hupp et al. 1996), and hence have been of limited applicability with respect to the importance of social context. Only by studying animals in their natural environment can we accurately measure the energy cost of social behavior in wild free-ranging birds.

LITERATURE CITED

BARTHOLOMEW, G. A. 1987. Interspecific comparison as a tool for ecological physiologists, p. 11–37. *In* M. E. Feder, A. F. Bennett, W. W. Burggren, and R. B. Huey [eds.], New directions in ecological physiology. Cambridge Univ. Press, Cambridge.

BURTON, B. A., R. J. HUDSON, AND D. D. BRAGG. 1979. Efficiency of utilization of bulrush rhizomes by Lesser Snow Geese. J. Wildl. Manage. 43:728–735.

BUTLER, P. J. 1991. Exercise in birds. J. Exp. Biol. 160:233–262.

BUTLER, P. J., AND D. L. TURNER. 1988. Effects of training on maximal oxygen uptake and caloric capacity of locomotory muscles in Tufted Ducks, *Aythya fuligula*. J. Physiol. 401:347–359.

BUTLER, P. J., AND A. J. WOAKES. 1979. Changes in heart rate and respiratory frequency during natural behavior of ducks, with particular reference to diving. J. Exp. Biol. 79:283–300.

BUTLER, P. J., AND A. J. WOAKES. 1980. Heart rate, respiratory frequency and wing beat frequency of free flying Barnacle Geese *Branta leucopsis*. J. Exp. Biol. 85:213–226.

ELY, C. R. 1992. Time allocation by Greater White-fronted Geese: influence of diet, energy reserves and predation. Condor 94:857–870.

ELY, C. R., AND A. X. DZUBIN. 1994. Greater White-fronted Goose (*Anser albifrons*). *In* A. Poole and F. Gill [eds.], The birds of North America, No. 131. The Academy of Natural Sciences, Philadelphia, and The American Ornithologists' Union, Washington, DC.

ELY, C. R., AND D. G. RAVELING. 1989. Body condition and weight dynamics of wintering Greater White-fronted Geese. J. Wildl. Manage. 53:80–87.

FREDERICK, R. B., AND E. E. KLAAS. 1982. Resource use and behavior of migrating Snow Geese. J. Wildl. Manage. 46:601–614.

GESSAMAN, J. A. 1980. An evaluation of heart rate as an indirect measure of daily energy metabolism of the American Kestrel. Comp. Biochem. Physiol. 65A:273–289.

HARMS, C. A., W. J. FLEMING, AND M. K. STOSKOPF. 1997. A technique for dorsal subcutaneous implantation of heart rate biotelemetry transmitters in Black Ducks: application in an aircraft noise response study. Condor 99:231–237.

HUPP, J. W., R. G. WHITE, J. S. SEDINGER, AND D. G. ROBERTSON. 1996. Forage digestibility and intake by Lesser Snow Geese: effects of dominance and resource heterogeneity. Oecologia 108:232–240.

JOHNSGARD, P. A. 1965. Handbook of waterfowl behavior. Cornell Univ. Press, Ithaca, NY.

KANWISHER, J. W., T. C. WILLIAMS, J. M. TEAL AND K. O. LAWSON JR. 1978. Radiotelemetry of heart rates from free-ranging gulls. Auk 95:288–293.

KORSCHGEN, C. E., K. P. KENOW, A. GENDRON-FITZPATRICK, W. L. GREEN, AND F. J. DEAN. 1996. Implanting intra-abdominal radio transmitters with external whip antennas in ducks. J. Wildl. Manage. 60:132–137

LAZARUS, J. 1978. Vigilance, flock size, and domain of danger in the White-fronted Goose. Wildfowl 29:135–146.

NAGY, K. A. 1987. Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57:111–128.

NOLET, B. A., P. J. BUTLER, D. MASMAN, AND A. J. WOAKES. 1992. Estimation of daily energy expenditure from heart rate and doubly labeled water in exercising geese. Physiol. Zool. 65:1188–1216.

PAYNTER, R. A., JR. [ED.]. 1974. Avian energetics. Nuttall Ornithol. Club, Cambridge, MA.

RAVELING, D. G. 1969. Preflight and flight behavior of Canada Geese. Auk 86:671–681.

SAS INSTITUTE. 1989. SAS/STAT user's guide. Release 6.04 ed. SAS Institute Inc., Cary, NC.

WALSBERG, G. E. 1983. Avian ecological energetics, p. 161–220. In D. S. Farner and J. R. King [eds.], Avian biology. Vol. 7. Academic Press, New York.

WEATHERS, W. W., W. A. BUTTERMER, A. M. HAYWORTH, AND K. NAGY. 1984. An evaluation of time-budget estimates of daily energy expenditure in birds. Auk 101:459–472.

WOAKES, A. J., AND P. J. BUTLER. 1983. Swimming and diving in Tufted Ducks, Aythya fuligula, with particular reference to heart rate and gas exchange. J. Exp. Biol. 107:311–329.

WOOLEY, J. B., JR., AND R. B. OWEN JR. 1977. Metabolic rates and heart rate-metabolism relationships in the Black Duck (Anas rubripes). Comp. Biochem. Physiol. 57:363–367.

WOOLEY, J. B., JR., AND R. B. OWEN JR. 1978. Energy costs of activity and daily energy expenditure in the Black Duck. J. Wildl. Manage. 42:739–745.

VOCALIZATIONS OF THE KITTLITZ'S MURRELET[1]

THOMAS I. VAN PELT AND JOHN F. PIATT
Alaska Biological Science Center, U.S. Geological Survey, 1011 East Tudor Road, Anchorage, AK 99503,
e-mail: thomas_van_pelt@usgs.gov

GUSTAAF B. VAN VLIET
P.O. Box 210442, Auke Bay, AK 99821

Abstract. We present the first documentation of Kittlitz's Murrelet (Brachyramphus brevirostris) vocalizations, based on recordings made in Glacier Bay, Alaska, in 1994. We identified two apparently related types of calls: groan and quack. The Kittlitz's Murrelet calls were markedly different from the most common calls of the congeneric Marbled Murrelet (Brachyramphus marmoratus), but shared characteristics with the Marbled Murrelet's less common "groan" call. Phylogeny, breeding biology, and habitat characteristics may explain relationships between the congeneric vocalizations. More complete knowledge of the Kittlitz's Murrelet vocal repertoire is needed before vocalizations can be either used or discarded in the design of effective programs to monitor this rare and poorly-known species.

Key words: Alaska, Alcidae, Brachyramphus brevirostris, calls, communication, Kittlitz's Murrelet.

The Kittlitz's Murrelet (Brachyramphus brevirostris) is a rare North Pacific alcid whose breeding biology and behavior remain obscure. Limited data suggest a world population of only about 20,000 birds (van Vliet 1993). Federal listing of the Kittlitz's Murrelet as a species of special concern in Alaska highlights the vulnerability of this species to oil pollution, gill-netting, and trophic changes (van Vliet and McAllister 1994). Because the Kittlitz's Murrelet has cryptic breeding plumage and breeds solitarily in remote alpine habitats

(Day et al. 1983), it is an exceptionally difficult species to monitor or manage.

Unlike its congener the Marbled Murrelet (Brachyramphus marmoratus), whose conspicuous vocal activity and extensive repertoire have been reasonably well described (Nelson and Hamer 1995, Nelson 1996), the vocal repertoire of the Kittlitz's Murrelet is virtually unknown; indeed, it is one of the last species within the North American avifauna whose voice has remained unrecorded. Webster (1950) gave the only known description of the Kittlitz's Murrelet call, referring to it briefly as "a hoarse, long-drawn-out squawk." Here we provide a more thorough description of the voice of the Kittlitz's Murrelet based on the first known audio recordings obtained for the species.

METHODS

We recorded alternate-plumaged Kittlitz's Murrelets at sea on the morning of 4 August 1994 from a 6-m vessel in Johns Hopkins Inlet (58°54′N, 137°02′W), Glacier Bay National Park, Alaska. We used a Sony TCD-D7 DAT recorder and a Sennheiser ME-88 shotgun microphone with a K3U power supply. Sonograms were produced on a Macintosh computer using Canary bioacoustics software, version 1.2.1 (Cornell Laboratory of Ornithology, Ithaca, New York). Vocalizations have been archived at the Library of Natural Sounds, Cornell Laboratory of Ornithology.

We drifted among small numbers (<10) of foraging Kittlitz's Murrelets for about 5 hr, and heard only a few vocalizations. Calling birds did not open their bills when vocalizing, but occasionally could be identified by distention of the gular region.