

Foraging patterns vary with the degree of sociality among Common Loon (*Gavia immer*) overwintering on a freshwater lake

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Abstract

Little is known about the behaviour of Common Loon (*Gavia immer*) during the critical overwintering period, let alone the behaviour of the small, but increasing number of loons that overwinter on freshwater lakes in North America. We examined the diurnal time-activity budgets of Common Loon overwintering on a large reservoir in northwest South Carolina between 2018 and 2020. Similar to previous studies of breeding individuals and individuals that overwinter in marine waters, loons ($n = 132$) overwintering on this reservoir spent most of their time (52%) foraging. However, we found distinct differences in the activity budgets of individuals associated with their degree of sociality. Solitary birds (individuals spending 0–20% of time within 20 m of conspecifics) spent significantly more time foraging than did those that were either loosely-social (>20–<70% of time within 20 m of conspecifics) or strongly-social (70–100% of time). Although solitary loons made as many foraging dives as social birds, their dives were much longer, likely reflecting dives for larger predatory fish. In contrast, social individuals made much shorter, shallower dives, often foraging on shallower baitfish that they appear to pursue to the water surface and consume collectively. Such findings add to our understanding of loon winter behaviour and raise interesting questions regarding social behaviour and the short- and long-term trade-offs associated with social foraging in this species.

Key words: Common Loon; *Gavia immer*; wintering behaviour; sociality

Introduction

Seasonal changes in the behaviour of many birds often correspond to shifting individual needs and environmental conditions during breeding, migrating, and overwintering (Jachowski and Singh 2015; Pasquier 2019). Common Loon (*Gavia immer*) is a long-lived waterbird that defends all-purpose territories on freshwater lakes throughout parts of the northern United States, Canada, and Greenland during the breeding season, but overwinters primarily on coastal and offshore marine waters of North America and Europe (McIntyre 1988; Paruk *et al.* 2021a). As visual underwater pursuit predators, adults spend approximately half of daylight hours during the breeding season foraging for fish and invertebrates to meet the extensive energetic requirements for themselves and their chicks (Evers 1994; Mager 1995; Paruk 1999; Nocera and Taylor 2000; Gingras and Paszkowski 2006). However, relatively little is known

about their overwintering behaviour. Behavioural scan samples of small overwintering groups indicate that foraging time varies greatly with location, ranging from 23 to 38% of daily activities off the coast of Rhode Island (Daub 1989; Ford and Gieg 1995) to 55 to 68% off the coast of Virginia (McIntyre 1978) and Florida (Vlietstra 2000). While such dissimilarities may result, in part, from differences in sampling protocols (Nocera and Taylor 2000), they may also reflect variation in foraging strategies associated with individual needs and/or variability of regional environmental conditions. These overwintering strategies are important to understand because of the foraging challenges and other threats posed by marine environments. The threats include increased predation risk (Vlietstra 1998) and exposure to pathogens and parasites (e.g., White *et al.* 1976; Kinsella and Forrester 1999; Sidor *et al.* 2003), biotoxins (McKernan and Scheffer 1942), and environmental contaminants

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such as oil (e.g., Camphuysen *et al.* 2010) and mercury (e.g., Alexander 1991). In addition, possible synergistic effects (e.g., Forrester *et al.* 1997; Augspurger *et al.* 1998) may affect overwintering survival (see review by Spitzer 1995) as well as the ability of individuals to prepare for the ensuing challenges of a protracted spring migration (Kenow *et al.* 2002; Gray *et al.* 2014).

A small, yet increasing number of loons are choosing to overwinter on freshwater lakes and reservoirs in North America rather than in marine waters (Clapp *et al.* 1982; Kenow *et al.* 2002, 2009; Campbell *et al.* 2008; Paruk *et al.* 2014, 2021b; Meehan *et al.* 2018), and these numbers are predicted to increase over the next few decades with a changing climate (e.g., Langham *et al.* 2015a,b). In the advent of these changes, it is important to better understand the activities of loons using freshwater lakes and how these behaviours may affect short- and long-term health of loon populations. Initial observations indicate that, unlike loons that overwinter in marine habitats, loons on freshwater lakes exhibit a high degree of sociality, which may be associated with different environmental conditions such as increased lake clarity and high abundance of forage fish that favour group foraging (Paruk *et al.* 2021b). However, we lack a basic understanding of the diurnal activities of these individuals, whether these behaviours differ substantially from those observed during the breeding season or while overwintering on marine waters, and whether they vary with the degree of sociality.

We studied the diurnal time-activity budgets of loons overwintering on a freshwater reservoir in northwest South Carolina. Our objectives were to: 1) determine the percent time individuals dedicate to various behaviours, 2) quantify the frequency and duration of their individual foraging dives, 3) conduct preliminary examinations of whether loon behaviour varies with time of day and geographic location, and 4) compare/contrast the activities of loons, including dive frequencies, durations, and frequencies of vocalizations they gave when solitary or with conspecifics.

Study Site

The State of South Carolina, in partnership with Duke Energy, created Lake Jocassee (34.9813°N, 82.9233°W; Figure 1). The lake incorporates a watershed area of 383 km², has a surface area of ~30 km², and a maximum depth at 107 m (mean 48 m) at a surface elevation of 340 m (Rodriguez 2013). Most of Lake Jocassee's roughly 121 km of shoreline is undeveloped, surrounded mostly by natural areas and state parks. Only 37 private residences exist along the lakeshore, concentrated near the southwestern arm of the Whitewater River and south of the dam. Duke Energy

has divided Lake Jocassee into four ecological zones (Figure 1) where surface temperature and average water depth, chlorophyll *a* concentration and density of zooplankton (within 10 m of the water surface), and forage fish are measured (Rodriguez 2013).

Lake Jocassee appears to be a highly suitable overwintering loon habitat: it is an extremely oligotrophic (lake wide total phosphorus concentration of <0.0055 mg/L and total nitrogen of <0.1510 mg/L; Rodriguez 2013), monomictic lake stocked annually with predatory Rainbow Trout (*Oncorhynchus mykiss*) and Brown Trout (*Salmo trutta*; Rodriguez 2013). These fishes, as well as Redeye Bass (*Micropterus coosae*) and Largemouth Bass (*Micropterus salmoides*), feed on a planktivorous pelagic forage fish community consisting of ~75% Blueback Herring (*Alosa aestivalis*) and ~25% Threadfin Shad (*Dorosoma petenense*) introduced into Lake Jocassee in the early 1970s (Davis and Foltz 1991; Rodriguez 2013). In contrast to Blueback Herring, Threadfin Shad are sensitive to lower water temperatures in that they can become immobilized at temperatures below 14°C and experience significant die-offs at temperatures below 9–12°C (Griffith 1978 cited in Rodriguez 2013). Consequently, the size of the forage fish community is positively correlated with the minimum winter surface water temperatures that can drop to 9–11°C between January and February (Rodriguez 2013).

Lake Jocassee is an overwintering site for roughly 125–150 Common Loon (from whole-lake surveys, we counted 150 individuals in 2018, 151 individuals in 2019, and 138 in 2020) as well as a staging site for many more individuals during spring and fall migration (as many as 1000 individuals in a single day during spring 'fallouts' due to poor weather; B.W. pers. obs.). Generally, loons begin to arrive on Lake Jocassee in mid-October and many remain throughout the winter when adults complete their prebasic moult with a synchronous remigial moult and later complete their definitive prealternate moult (Woolfenden 1967; Paruk *et al.* 2021a). Loons are seen on the lake until mid-April although non-breeding juveniles and adults are observed occasionally on the lake in late spring and summer. The distribution of loons that overwinter on Lake Jocassee does not appear to be random: greater densities (40.2 ± 2.7 [SE] loons/km²) are found in zone 4 (Figure 1) than in zone 2 (19.5 ± 1.7) and zone 1 (18.5 ± 4.0 , the main basin), which are greater than those in zone 3 (4.5 ± 0.4 ; Paruk *et al.* 2021b). As has been seen at other wintering areas (Paruk *et al.* 2015), loons exhibit high winter site fidelity on Lake Jocassee. We observed nine of the 10 loons we banded on Lake Jocassee in subsequent years and each was re-observed in the same lake zone.

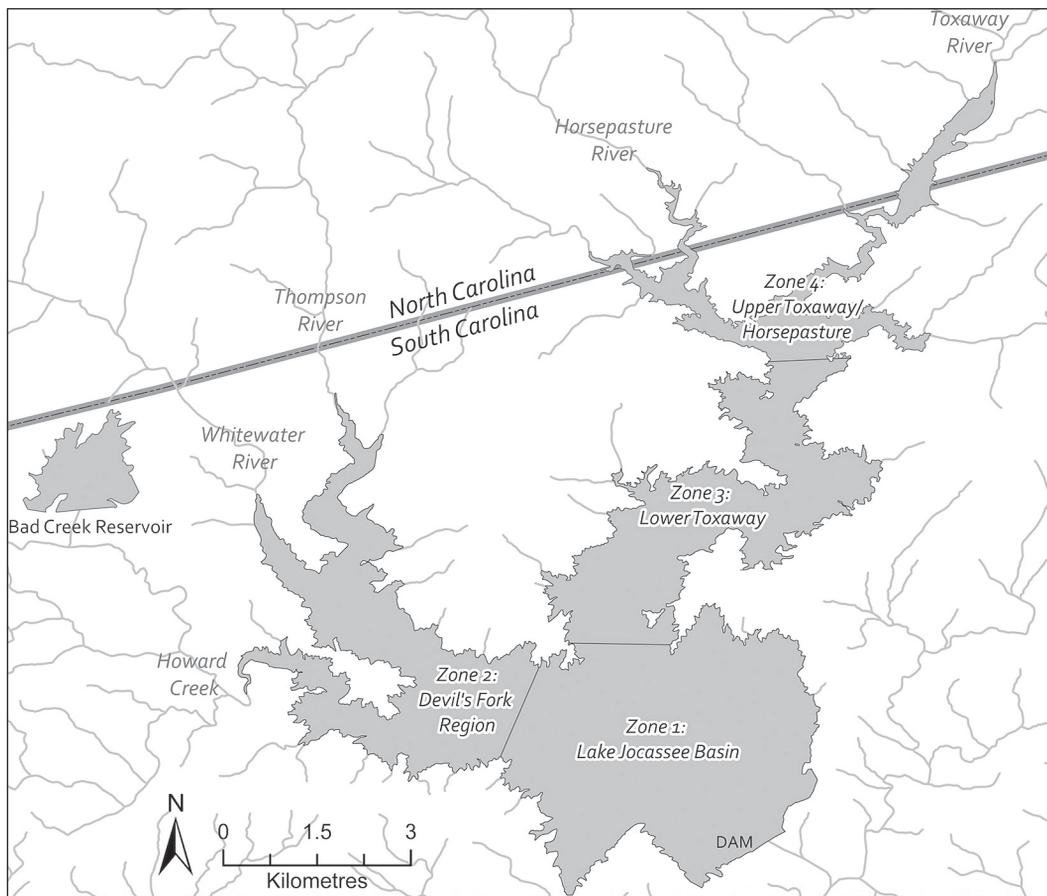


FIGURE 1. Map of Lake Jocassee, South Carolina, indicating the four main geographic zones Duke Energy established (Rodriguez 2013).

Methods

Behavioural sampling

We examined the behaviour of 132 individual loons between January and March for three successive years (2018–2020). Using teams of 3–7 observers, we generated time-activity budgets from 30 2-min instantaneous scan samples on each focal bird over a 1-h observation period between 0700 and 1815 h from either boat or shore throughout all regions of the lake. We only lost sight of individuals during 16 of the 132 observation periods; of these the mean number of scan samples for which we could not locate focal individuals was 2.6 (~5 min). We identified and tracked individuals based on either distinctive plumage patterns ($n = 127$) or a unique combination of coloured leg bands ($n = 5$; see Strong *et al.* 1987) from our banding efforts (see Evers 1993 for protocol). To minimize the likelihood of conducting 1-h observations of the same unbanded individual twice,

we sampled birds with individually distinct plumages from different zones or regions within each zone each day. Although we conducted repeated observations of banded individuals within each year and over multiple years, we only included the most recent behavioural sample for banded individuals in our analyses to minimize non-independence of individual samples even when the same individual was observed over multiple years. It is still possible that over the three years we observed the same individual twice even though we tried to minimize potential repeated sampling.

At each instantaneous 2-min scan sample, we recorded the individual's behaviour (foraging, locomotion, resting, self-maintenance, agonistic; see Table 1), the distance between the bird and the nearest conspecific (in loon 'body lengths', equivalent to 0.75 m, following del Hoyo *et al.* 1992), and, if the focal individual was within 20 m of other loons, the number of conspecifics in a social group (i.e., within 20 m of a

TABLE 1. Definitions of Common Loon (*Gavia immer*) behaviours.

Behavioural state	Description/definition
Foraging	Periods of sustained diving (<30 s intervals between dives) by individuals.
Locomotion	Surface swimming, involving active paddling of legs that created a noticeable wake in water.
Resting	Drifting on the surface of the water with little paddling of legs. Includes periods of sleeping with head tucked into back of body.
Self-maintenance	Includes periods of activities associated with preening and bathing.
Agonistic	Includes periods of aggression, e.g., vulture posturing, active chasing, and/or lunging toward conspecific or interspecific individuals.

conspecific). During each 1-h observation period, we continuously recorded the occurrence and duration (to the nearest s) of each focal individual's underwater dive and counted the number of audible vocalizations (hoots, mews, wails, tremolos, and yodels; see Paruk *et al.* 2021a) that focal individuals ('individual' vocalizations) or individuals within 20 m of focal individual (i.e., 'group' vocalizations) produced. We recorded the latitude and longitude, surface water and air temperature at the beginning and end of each 1-h observation period, and, weather permitting, the Secchi depth of water clarity at our location.

Analysis

We calculated individual time-activity budgets by determining the proportion of the 2-min instantaneous scan samples within the 1-h observation period individuals spent in each behaviour and calculated the frequency (#/h) and mean duration (to the nearest s) of dives. We examined all behavioural data for normality with the Shapiro-Wilk Goodness-of-fit Test and, when appropriate, normalized time-activity budget proportions by logit-transformation by adding minimum non-zero proportion to both the numerator and denominator functions of the transformation to prevent transformations to undefined values of ∞ and $-\infty$ when proportion values were equal to 0 or 1, respectively (Warton and Hui 2011; Douma and Weedon 2018), although we present proportions as non-transformed values. We used factorial analysis of variance (ANOVA) and corresponding *post hoc* tests to examine differences in loon activities among periods of the day: early morning (0700–0915), late morning (0916–1130), afternoon (1131–1345), late afternoon (1346–1600), and early evening (1601–1815), following Vlietstra (1998). We also used factorial ANOVA to examine differences in the behaviour of individuals in the four zones. We used JMP version 14.3 (2018, SAS Institute, Cary, North Carolina, USA) for all descriptive and analytical procedures and accepted experiment-wide statistical significance at $P < 0.05$. We report values as means (\bar{x}) \pm SE.

Results

Activity budgets of individual Common Loons overwintering on Lake Jocassee

Individual loons ($n = 132$) overwintering on Lake Jocassee spent most of their time foraging ($52.2 \pm 2.4\%$), followed by locomotion ($19.9 \pm 1.4\%$), resting ($16.8 \pm 1.6\%$), and self-maintenance ($11.2 \pm 1.1\%$). They spent an extremely small amount of time ($0.08 \pm 0.05\%$) in agonistic activities and did not display any territorial behaviour. The proportion of time individuals dedicated to these activities did not differ with time of day ($F_{4,127} \leq 1.5$, $P \geq 0.21$ for all comparisons) nor among the four zones in Lake Jocassee ($F_{3,128} \leq 2.0$, $P \geq 0.12$ for all comparisons). On average, individuals dove 23.1 ± 1.3 /h (range 0–90) with an average dive duration of 55.8 ± 2.1 s (range 9.2–134.0). Both the frequency ($F_{4,123} = 1.1$, $P = 0.36$) of diving and the duration of dives ($F_{4,121} = 0.62$, $P = 0.65$) did not vary with time of day. Most of the 1.0 ± 1.0 vocalizations/h were hoots (2.9 ± 1.07 /h) and mews (0.9 ± 0.8 /h), but individuals also produced, albeit infrequently, wails (0.1 ± 0.0 /h), tremolos (0.1 ± 0.1 /h), and yodels (0.01 ± 0.01 /h).

Collectively, loons spent $43.7 \pm 3.3\%$ of their time within 20 m of conspecifics. The size of conspecific groups varied between two and 18 individuals (average group size for each focal individual weighted by time spent in each group = 3.55 ± 0.15 individuals; median = 3; Figure 2). The proportion of time an individual spent in groups was not related to the time of day ($F_{4,127} = 1.49$, $P = 0.21$) nor with water clarity ($F_{1,55} = 0.03$, $P = 0.86$). However, those individuals ($n = 89$) that spent part of the observation period both alone (>20 m from a conspecific) and with other loons (<20 m) spent significantly more time foraging ($P = 0.0002$) and made longer dives ($P < 0.001$) when solitary than when they were part of a group, but did not differ in the rates they gave each type of vocalization (Table 2).

There were distinct differences in the degree of sociality among individuals as shown by the distribution of the proportion of the 1-h observation

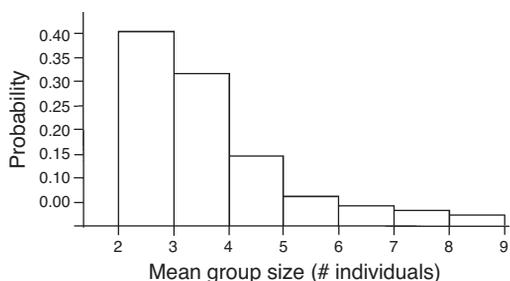


FIGURE 2. Probability distribution of mean group size, weighted by proportion time spent within 20 m of various numbers of conspecifics, of individual Common Loon (*Gavia immer*) overwintering on Lake Jocassee, South Carolina, 2018–2020.

period the population spent <20 m of a conspecific. We could best categorize these individuals into three groups based upon the means and inflection points of a best fit 3-normal mixture ($-2 \times \text{Log-likelihood} = 2.62$; $\text{AIC}_c = 19.79$; Figure 3) generated from an examination of all available continuous models (normal, 2-normal mixture, 3-normal mixture, exponential, sinh-arcsinh normal, Johnson-Su, and GLog) with JMP version 14.3. ‘Solitary’ individuals spent a relatively small percent (0–20%, $\bar{x} = 3.92\%$, $n = 53$) of daily activities <20 m from conspecifics and rarely, if ever, approached nearby conspecifics. Other individuals exhibited a degree of sociality in which they were drawn to, and interacted with conspecifics during the observation period, but could be differentiated into two groups based upon the duration of time they spent with conspecifics. Strongly social birds spent

a relatively high percent (70–100%, $\bar{x} = 90.10\%$, $n = 46$) of their time with conspecifics, rarely spending any time alone, while ‘loosely-social’ individuals, spent a moderate percent (>20–<70%, $\bar{x} = 45.46\%$, $n = 33$) of their time with conspecifics but also spent time alone.

Although solitary, loosely-social, and strongly-social individuals inhabited each zone, the distribution of these individuals varied across the four geographic zones of the lake (Pearson $\chi^2_6 = 22.66$, $n = 132$, $P < 0.001$; Table 3). Equal numbers of solitary and social individuals inhabited zones 1 and 3 while more of the lake’s social individuals inhabited zones 2 and 4. A greater proportion of individuals we observed in Zones 1 and 3 of Lake Jocassee were solitary and thus the proportion of time these individuals were <20

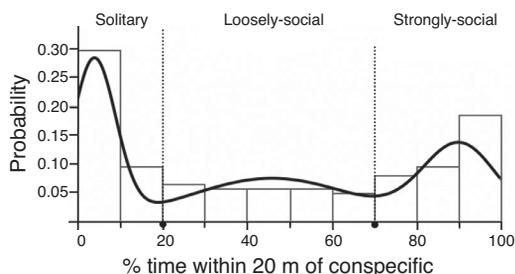


FIGURE 3. Probability distribution of the proportion of time Common Loon (*Gavia immer*; $n = 132$) overwintering at Lake Jocassee, South Carolina, spent within 20 m of a conspecific, with superimposed best fit 3-normal distribution (solid curve) and separation of individuals into solitary, loosely-social, and strongly-social categories based upon inflection points of this curve.

TABLE 2. Paired comparisons of the mean (± 1 SE) percent of time individual Common Loon (*Gavia immer*; $n = 93$) dedicated to behavioural states, dive frequencies, dive durations, and frequencies of calls given when solitary and when in a conspecific group (<20 m).

Parameter	Solitary (>20 m)	Group (<20 m)	t *	P
Foraging (% time)	61.9 \pm 2.9	45.9 \pm 3.4	3.94	0.0002
Locomotion (% time)	17.6 \pm 2.0	25.7 \pm 2.7	1.92	0.0577
Resting (% time)	11.5 \pm 2.2	16.3 \pm 2.4	1.17	0.2452
Self-maintenance (% time)	8.9 \pm 1.4	12.1 \pm 1.8	1.29	0.2013
Agonistic (% time)	0.0 \pm 0.0	0.2 \pm 0.2	1.00	0.3200
Dive rate (#/h)	24.2 \pm 1.4	26.6 \pm 2.7	0.83	0.4070
Dive duration (s)	63.3 \pm 2.6	40.4 \pm 2.6	8.41	<0.0001
Call rate (#/h)	2.2 \pm 0.4	2.9 \pm 1.2	0.55	0.5855
Hoot rate (#/h)	2.0 \pm 0.4	1.7 \pm 0.4	1.05	0.2946
Mew rate (#/h)	0.2 \pm 0.1	1.2 \pm 1.2	0.88	0.3809
Wail rate (#/h)	0.06 \pm 0.03	0.05 \pm 0.04	0.03	0.9782
Tremolo rate (#/h)	0.02 \pm 0.02	0.00 \pm 0.00	1.00	0.3199
Yodel rate (#/h)	0	0	—	—

*Values would be negative in cases where Group > Solitary.

TABLE 3. Limnological measurements and behavioural differences among individual Common Loon (*Gavia immer*) inhabiting each zone of Lake Jocassee, South Carolina, 2018–2020.

Parameter	Zone 1	Zone 2	Zone 3	Zone 4	<i>F</i>	df	<i>P</i>
Limnological parameter*							
\bar{x} Depth (m)	57.7	44.7	47.4	36.1			
\bar{x} Min. surface temp. (°C)	9.9	10.2	10.2	10.1			
\bar{x} Chl <i>a</i> @ 0–10 m (mg/m ³)	1.79	2.18	2.37	3.10			
\bar{x} Total zooplankton (#/m ³)	13 167	10 601	19 374	21 014			
\bar{x} Fall forage fish density (#/ha)	1360	608	1077	2744			
\bar{x} Surface water temp (°C)	11.3 ± 0.1	11.6 ± 0.1	11.3 ± 0.2	11.7 ± 0.1	2.54	3,118	0.0500
\bar{x} Secchi depth (m)	6.66 ± 0.28	6.28 ± 0.24	6.05 ± 0.32	5.08 ± 0.25	6.68	3,53	0.0007
# Individuals by social type	49	38	18	27			
# Solitary	25	11	10	7			
# Loosely-social	13	4	6	10			
# Strongly-social	11	23	2	10			
Behavioural state							
\bar{x} Foraging (% time)	45.6 ± 3.9	52.5 ± 4.4	59.9 ± 6.5	58.9 ± 5.3	1.52	3,128	0.2114
\bar{x} Locomotion (% time)	23.9 ± 2.4	19.0 ± 2.7	18.2 ± 4.0	15.5 ± 3.2	2.01	3,128	0.1160
\bar{x} Resting (% time)	18.3 ± 2.6	17.3 ± 3.0	15.4 ± 4.46	12.8 ± 3.6	0.46	3,128	0.7111
\bar{x} Self-maintenance (% time)	11.6 ± 1.9	12.0 ± 2.1	6.2 ± 3.1	12.7 ± 2.5	1.38	3,128	0.2523
\bar{x} Agonistic (% time)	0.14 ± 0.09	0.00 ± 0.11	0.00 ± 0.16	0.13 ± 0.13	0.47	3,128	0.7030
<20 m of conspecific (% time)	34.3 ± 5.0	59.9 ± 5.7	28.9 ± 8.3	49.82 ± 6.81	4.77	3,121	0.0035
Dive frequency (#/h)	17.90 ± 2.10	25.01 ± 2.40	21.49 ± 3.44	30.62 ± 2.81	4.68	3,125	0.0039
Dive duration (s)	57.70 ± 3.80	51.68 ± 4.20	69.00 ± 6.19	49.98 ± 4.91	2.38	3,122	0.0448

*From Gutierrez (2013).

m of a conspecific was significantly lower than individuals we observed in zones 2 and 4 (Table 3).

Solitary individuals spent more time foraging than both loosely-social individuals ($t_{129} = 2.45$, $P = 0.0158$) and strongly-social ($t_{129} = 4.82$, $P < 0.0001$; Table 4) individuals. Although solitary individuals dove as often as social individuals, their dives were much longer than those of loosely-social ($t_{123} = 2.77$, $P < 0.01$) and strongly-social ($t_{123} = 6.22$, $P < 0.0001$) individuals (Table 4). Solitary individuals also spent significantly less time in locomotion ($t_{129} = 3.91$, $P < 0.0001$), resting ($t_{129} = 2.55$, $P = 0.02$), and self-maintenance ($t_{129} = 2.13$, $P = 0.04$) activities in comparison to strongly-social individuals (Table 4). Both types of social individuals dove as frequently as solitary individuals, but made shorter dives, often feeding as groups upon schools of Bluefin Herring and Threadfin Shad that came to the water surface. Among social individuals, loosely-social individuals spent more time foraging ($t_{129} = 1.87$, $P = 0.03$) and made longer foraging dives ($t_{123} = 2.75$, $P < 0.01$) than strongly-social individuals, but invested less time in self-maintenance ($t_{129} = 2.26$, $P = 0.03$; Table 4). There was

no difference in the rate each type (solitary, loosely-social, and strongly-social) of individual vocalized (Table 4).

Discussion

Suitability of freshwater habitats for overwintering loons

Similar to the habitats they select for breeding (Hammond *et al.* 2012) and migrating (Kenow *et al.* 2018), loons likely select overwintering sites that meet the substantial foraging requirements of a visual underwater pursuit predator. These tend to be shallow areas (e.g., <35 m; Winiarski *et al.* 2013) of lower turbidity (e.g., Haney 1990; Thompson and Price 2006) and moderate productivity (e.g., chlorophyll *a* concentration >2 mg/m³; Winiarski *et al.* 2013). The clearer waters of southern inland lakes with large forage fish communities such as Lake Jocassee provide suitable, if not ideal habitat for overwintering loons. Individuals choosing to overwinter on freshwater lakes would be exposed to fewer predators (particularly from underwater), possibly a different array of

TABLE 4. Mean (± 1 SE) time dedicated to various behavioural states, and mean (± 1 SE) dive frequencies, dive durations, and call frequencies of solitary, loosely-social, and strongly-social Common Loon (*Gavia immer*) overwintering at Lake Jocassee, South Carolina, 2018–2020.

Parameter	Solitary (<i>n</i> = 53)	Loosely-social (<i>n</i> = 33)	Strongly-social (<i>n</i> = 46)	<i>F</i>	df	<i>P</i>
Foraging (% time)	63.2 \pm 3.5	54.5 \pm 4.5	38.0 \pm 3.8	11.64	2,129	<0.0001
Locomotion (% time)	13.8 \pm 2.2	21.1 \pm 2.8	26.1 \pm 2.4	8.08	2,129	0.0005
Resting (% time)	12.9 \pm 2.5	16.5 \pm 3.2	20.6 \pm 2.7	3.08	2,129	0.0494
Self-maintenance (% time)	10.0 \pm 1.7	7.5 \pm 2.2	15.3 \pm 1.9	3.28	2,129	0.0410
Agonistic (% time)	0.00 \pm 0.09	0.30 \pm 0.10	0.00 \pm 0.10	2.96	2,129	0.0555
Dive rate (#/hr)	22.8 \pm 2.2	24.7 \pm 2.7	22.6 \pm 2.3	0.21	2,125	0.8130
Dive duration (sec)	69.5 \pm 3.2	55.1 \pm 4.1	40.4 \pm 3.4	19.20	2,123	<0.0001
Call rate (#/hr)	2.5 \pm 0.7	5.1 \pm 1.5	4.9 \pm 2.5	0.78	2,129	0.4621
Hoot rate (#/hr)	2.2 \pm 0.8	4.6 \pm 1.0	2.4 \pm 0.9	1.98	2,129	0.1428
Mew rate (#/hr)	0.06 \pm 0.05	0.31 \pm 0.31	2.41 \pm 2.39	0.83	2,129	0.4382
Wail rate (#/hr)	0.10 \pm 0.04	0.09 \pm 0.07	0.11 \pm 0.08	0.02	2,129	0.9834
Tremolo rate (#/hr)	0.14 \pm 0.14	0.09 \pm 0.07	0.00 \pm 0.00	0.54	2,129	0.5859
Yodel rate (#/hr)	0.02 \pm 0.02	0.00 \pm 0.00	0.00 \pm 0.00	0.63	2,129	0.5354

parasites and potential pathogens, and may also experience lower metabolic costs, such as those posed from maintaining active salt glands that could indirectly hamper growth, immunocompetence, moult, and accumulation of fuel reserves sufficient for migration (e.g., Gutiérrez *et al.* 2011; Gutiérrez 2014). Individuals overwintering in freshwater lakes may also experience substantial carry-over benefits associated with migratory phenology and arrival time on breeding lakes as well as breeding performance and condition (e.g., Inger *et al.* 2010; Rotics *et al.* 2018). Because these associated short- and potentially long-term fitness advantages may be considerable, it is not surprising that more individuals are choosing to overwinter on freshwater lakes and reservoirs throughout much of North America, not just within the Piedmont and Southeastern Coastal Bird Conservation Regions (Meehan *et al.* 2018), that include Lake Jocassee. Further comparisons of the migratory phenology, physical health and condition, and reproductive success of these individuals with those that overwinter in marine habitats would facilitate more rigorous examinations of these potential benefits.

Time-activity budgets of loons wintering on Lake Jocassee

Collectively, the diurnal activity budgets of Common Loons overwintering on the clear, protected, and prey-rich waters of Lake Jocassee do not differ from those of loons on breeding lakes as well as from loons overwintering on marine waters along the coast of Virginia (McIntyre 1978), Florida (Vlietstra 1998, 2000), and Rhode Island (Daub 1989; Ford and Gieg 1995).

Individuals spent most of their time (~50% of daily activities) foraging and to a lesser extent among activities associated with resting, locomotion, and self-maintenance. Likewise, the collective frequencies and durations of dives made by loons on Lake Jocassee are similar to loons foraging on similar prey types on breeding (e.g., Reimchen and Douglas 1980; Alvo and Berrill 1992; Nocera and Burgess 2002; Gingras and Paszkowski 2006) and overwintering (e.g., Stewart 1967; Kinnear 1978; Dickson 1980) lakes. These findings are consistent with the notion that foraging is a large component of the daily activities of Common Loons (McIntyre 1988), and upon first glance may indeed be fixed (i.e., ~50% of daily activities) temporally within and between seasons (Nocera and Burgess 2002) to meet the energetic demands of these waterbirds.

However, closer inspection of these activity budgets on Lake Jocassee reveals the time loons spend foraging is flexible depending upon the foraging strategy they adopt. Similar to other piscivorous waterbirds (e.g., Kersten *et al.* 1991; McMahon and Evans 1992), the time loons on Lake Jocassee dedicate to foraging appears to vary significantly with their degree of social organization. Perhaps best exhibited by loosely-social loons, these behaviours likely reflect the dynamics of a fission-fusion social system (Silk *et al.* 2014) whereby they use a fluid, cooperative foraging strategy that involves shifts from uncoordinated individual foraging tactics with high inter-individual distance to highly coordinated, if not cooperative, group foraging tactics with low inter-individual distance to effectively harvest clumped aggregations of

feeder fish at the water surface. Other loons, however, appear to adopt a more strict social foraging strategy where they spend most, if not all of their daily time, including their time foraging, in a social group. These strongly-social individuals, more frequently observed within zones 2 and 4 within the reservoir, spend significantly less time foraging (~39%) but appear to cooperatively locate and consume large schools of small schooling fish that come to the water surface. As shown by their shorter foraging times, social individuals likely spend less time and energy to collectively search for, pursue, and catch multiple individuals within schools of smaller forage fish (thereby increasing individual foraging efficiency; e.g., Götmark *et al.* 1986) but must share access to the school of prey with conspecifics.

In contrast, solitary individuals found more frequently within zones 1 and 3, which include the more open Jocassee basin and the Lower Toxaway arms of Lake Jocassee, use a foraging strategy where they spend more time foraging (~64%) and make longer foraging dives. We believe solitary individuals are likely foraging for larger, more difficult to catch fish found in the deeper waters of Lake Jocassee, as longer dives among Common Loon are associated with this type of prey (Alvo and Berrill 1992; Barr 1996; Kenow *et al.* 2018). This is supported by our occasional observations of solitary loons surfacing at times with bass and trout, as well as Channel Catfish (*Ictalurus punctatus*) that are found at greater depths in Lake Jocassee. Such a solitary foraging strategy is physiologically costlier (see reviews by Butler and Jones 1997; Kooyman and Ponganis 1998; Butler 2000; Kenow *et al.* 2018) and likely results in lower intake rates (Butler 2000), but it also provides greater energetic benefits per intake. How these social and solitary foraging strategies help loons meet the changing metabolic demands of overwintering and preparing for spring migration merit further consideration of composition and intake rates of various prey types by individuals.

Such differences in foraging strategies may reflect inherent differences in body size, sex, personality type, and/or age, as well as differences in experience and body condition (see reviews by Giraldeau and Caracao 2000; Krause and Ruxton 2002; Sih *et al.* 2004). For example, although we did not detect such differences in our study, anecdotal differences in overwintering foraging behaviour between juveniles and adults have been observed in northern Europe (Byrkjedal 2011), as have shifts in the foraging depths of migratory female loons staging on the Laurentian Great Lakes (Kenow *et al.* 2018). Similarly, we currently do not know the migratory routes nor the locations where these individuals breed and

whether their overwintering foraging strategies are similar to those during the breeding season. Additionally, although our initial examinations did not find a relationship between foraging strategy type and primary productivity nor fall forage fish densities within each ecological zone of Lake Jocassee, closer examination of the availability and distribution of forage and predatory fish, as well as limnological features of specific regions within each zone is warranted, as foraging strategy may be related to these (e.g., Carr and MacDonald 1986; McMahan and Evans 1992; also see review by Krause and Ruxton 2002). Such possibilities warrant further examinations of the short- and long-term trade-offs associated with solitary and group foraging.

Sociality among overwintering loons

The degree of sociality loons exhibit during non-breeding seasons likely reflects trade-offs associated with the benefits and consequences of group living. Following the breeding season, Common Loon often congregate in large groups before (McIntyre 1983) and during (Powers and Cherry 1983; Evans *et al.* 1994; Kratter 2009) migration to overwintering sites. Because most (~90%; McIntyre 1978; Daub 1989; Ford and Gieg 1995; Vlietstra 2000) individuals that overwinter in coastal and offshore waters are largely alone and at times aggressive (Byrkjedal 2011, 2017), if not territorial (McIntyre 1978), it has been generalized that nonbreeding loons are mostly solitary (Crook 1965) and lack social organization (Matthysen 1993). However, loons overwintering in marine areas periodically aggregate in both small (two individuals) and large (200–1000 individuals) groups (Teulings 1973; Jodice 1993; Spitzer 1995; Vlietstra 2000; Byrkjedal 2011; Long and Paruk 2014). Selective advantages of group living within certain environmental and social conditions can include shared protection from winter storms (Stocking *et al.* 2018), protection from predation via dilution or distraction effects (Vlietstra 1998), and/or through enhanced vigilance against predation by sharks and large fishes (Vlietstra 1998, 2000). Indeed, such sociality may provide protective benefits (see reviews by Clark and Mangel 1986; Krause and Ruxton 2002; Davies *et al.* 2012) that should be examined further across this species' broad overwintering range.

Our study reveals that sociality may also provide significant foraging benefits to loons overwintering on freshwater lakes. Social foraging is believed to be adaptive when food is localized in patches and the detection of patches of food by flocks is greater than that by individuals (see reviews by Crook 1965; Pulliam and Millikan 1982). Indeed the foraging benefits associated with sociality may be particularly beneficial for loons overwintering on freshwater lakes,

such as Jocassee, where predation risks are extremely low and food resources, particularly foraging fish, are abundant and aggregately distributed. Loons likely experience increased benefits associated with cooperation and coordination of foraging for these schooling fish as group size increases; however, they also likely experience increased costs associated with competition for those fish (see reviews by Krause and Ruxton 2002; Davies *et al.* 2012). Although we observed little, if any, overt aggression among conspecifics, let alone any anecdotal increase in individual aggression with group size, closer examinations of how competitive and cooperative relationships between group members influence optimal group size under varying environmental conditions in this system, as well as within other marine and freshwater ecosystems during the breeding, migratory, and overwintering seasons, would be worth future exploration.

Conclusions

Freshwater lakes and reservoirs in southern North America, such as Lake Jocassee in South Carolina, potentially provide substantial, if not ideal habitats for overwintering Common Loon. As observed on breeding lakes as well as on marine environments, loons overwintering here forage for most of the day. However, these loons vary in their foraging behaviour in association with a degree of sociality that is not typically observed among loons overwintering in marine environments. Individuals that are strongly social, spending most of their time with conspecifics, spend less time foraging but make shorter dives, often collectively if not cooperatively, for forage fish that are found closer to the water surface. In contrast, other individuals on Lake Jocassee adopt a solitary strategy in which they rarely come within 20 m of a conspecific, spend a greater proportion of time foraging, but make longer dives, presumably for predatory fish that are found in deeper waters. Each strategy likely reflects each individual's abilities to optimally meet the metabolic demands associated with overwintering and preparing for spring migration; however, much research is needed to further evaluate the costs and benefits associated with each strategy. Lastly, we hope to look more closely at whether there are changes in the strategies of individuals from year to year or during the course of a winter by banding more birds and spending more time observing these marked individuals during the course of a winter.

Author Contributions

Writing – Original Draft: J.N.M.; Writing – Review & Editing: J.N.M., J.D.P., S.A., and B.W.; Conceptualization: J.N.M. and J.D.P.; Investigation: J.N.M., J.D.P., S.A., and B.W.; Methodology: J.N.M., J.D.P., S.A., and B.W.; Formal Analysis: J.N.M.;

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