logically limiting factor. In contrast, the observed correlation between body mass and temperature may be determined by a pattern of slow growth, which is part of a suite of life history parameters (delayed maturity, long life span) that are coupled with their complex social behavior (Bucher 1983).

We thank don Alfonso Madriñán for allowing us to work on his property. Carolina Murcia, Ron Edwards, Lou Guillette and an anonymous reviewer made comments that greatly improved the manuscript. During the realization of this project GK was supported by grants from the Colombian agencies Fundación para la Promoción de la Investigación y la Tecnología (Banco de la República, Bogotá) and Fondo de Investigaciones Científicas "Francisco José de Caldas" (COLCIENCIAS).

LITERATURE CITED

Bucher, T. L. 1983. Parrot eggs, embryos, and nestlings: patterns and energetics of growth and development. Physiological Zoology 56:465–483.

Bucher, T. L., and G. A. Bartholomew. 1986. The early ontogeny of ventilation and homeothermy in an altricial bird, *Agapornis roseicollis* (Psittaciformes). Respiration Physiology 65:197–212.

Case, T. J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Quarterly Review of Biology 53:243–282.

Forshaw, J. M. 1973. Parrots of the world. Doubleday, New York.

Gómez, N. 1991. Historia natural del Cascabelito (*Forpus conspicillatus*) en el Valle del Cauca. Tesis, Depto. de Biología, Universidad del Valle, Cali, Colombia.

Hill, R. W., and D. L. Beaver. 1982. Inertial thermostability and thermoregulation in broods of Red-winged Blackbirds. Physiological Zoology 55:250–266.

Olson, J. M. 1991. Thermal relations of nestling Red-winged Blackbirds in southeastern Michigan. Auk 108:711–716.

The Condor 94:282–286

DENSITY OF LOONS IN CENTRAL ALASKA[1]

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Key words: Common, Pacific, and Red-throated Loon; Yukon Flats National Wildlife Refuge; density; aerial survey; Alaska.

Loons breed across North America from the high arctic south to about 43° north latitude (AOU 1983). Populations, particularly of Common Loons (*Gavia immer*), have recently declined in the continental U.S. and southern Canada (Sutcliffe 1979, Titus and VanDruff 1981, McIntyre 1988). As a result, state and private natural resource organizations began more intensive monitoring of loon populations (in McIntyre 1986, Strong 1988). These surveys, however, are restricted to areas accessible by road, although recently aircraft were used for more remote areas (Lee and Arbuckle 1988, Strong 1990).

Previous studies of loons in remote areas of Canada and Alaska were primarily about reproductive behavior and nesting ecology, and have focused on small geographic areas (Munro 1945; Davis 1972; Petersen 1976, 1979; Sjölander and Ågren 1976; Bergman and Derksen 1977; Fox et al. 1980; Smith 1981; Yonge 1981; North 1986). Few studies specifically addressed abundance over large, remote portions of Canada and Alaska. Available data for these regions come primarily from studies which focused on other species or species-groups of waterbirds (e.g., U.S. Fish and Wildlife Service annual pairs counts of waterfowl). Errors in accuracy and precision are common in such multi-species surveys (Smit et al. 1981; Butler, U.S. Fish and Wildlife Service, pers. comm.). Annual Breeding Bird Surveys throughout Canada are another source of information, but again, are of limited value because only road surveys are conducted (McNicholl 1988). We know of only one unpublished study conducted specifically to assess the abundance of loons in Alaska (McIntyre, Utica College, in prep.).

Our goal was to design and conduct an aerial survey to estimate loon density over a large and remote area of central Alaska. Previously, we reported the aerial

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line transect methodology used in our survey (Quang and Lanctot 1991). Here we report results of our survey, discuss problems in comparing density estimates among other studies, and recommend procedures for standardizing aerial surveys.

STUDY AREA AND METHODS

We conducted our study on 1–2 June 1988 on the Yukon Flats region (a 2,600 km² area) of the Yukon Flats National Wildlife Refuge, Alaska. The Yukon Flats is about 240 km north of Fairbanks. The area has up to 40,000 wetlands and lowland lakes, most concentrated near tributaries of the Yukon River. Lakes are generally oval, less than 16 ha in size, with open shorelines, and often interconnected with streams. The area is considered prime breeding habitat for loons (U.S. Fish and Wildlife Service 1987). Our survey was conducted shortly after ice melted off lakes, when most loons were just beginning to nest. The extremely flat terrain and the stunted taiga forests allowed loons to be observed relatively easily.

Our survey was along 30 randomly selected 25.7 km long transects and used the methodology of Quang and Lanctot (1991). Transects were flown in a float equipped Cessna 185, 30 to 50 m above the ground at a speed of 167 km/hr. Perpendicular distances of loons from the plane path were derived from markers on the wing struts. These corresponded to distances of 25–75, 76–125, 126–175, and 176–225 m from the plane. We pooled observations of the pilot and both observers (i.e., loons observed on the left and right sides of the plane, respectively). A comparative ground study was not conducted. All density estimates are presented as loons/km² of land area (± standard deviation).

RESULTS

The density of Pacific Loons (*G. pacifica*) was 0.49 ± 0.10 and for Common Loons was 0.12 ± 0.06. These densities resulted in a population estimate for the entire Yukon Flats of 12,740 ± 2,600 Pacific Loons and 3,120 ± 1,560 Common Loons. Only three Red-throated Loons (*G. stellata*) were seen during the survey. When we included sightings of unidentified birds (most of which were diving loons that we could not identify to species), the total density of all species of loons was 0.76 ± 0.15, and our projected population of the Yukon Flats was 19,760 ± 3,900 loons.

DISCUSSION

We believe our estimated densities of loons on the Yukon Flats are fairly accurate because Petersen mark-and-recapture methodology yielded similar estimates and computer simulation trials indicated the implemented line transect model was robust (Quang and Lanctot 1991). We could not, however, directly compare our results with other studies, since this was the first time aerial line transect methodology was used to survey loons and because no other loon surveys had ever been conducted on the Yukon Flats (Table 1).

Crude comparisons between our study and others, however, indicate the Yukon Flats National Wildlife Refuge is a relatively important breeding area for Pacific Loons and possibly for Common Loons. Similar densities of Pacific Loons were found on the Arctic Coastal Plain of Alaska (King 1979, unpubl. data), but higher densities occur on the Yukon-Kuskokwim Delta of Alaska (Petersen 1976) and near the McConnell River of the Northwest Territories, Canada (Davis 1972) (Table 1). Our density of Common Loons was much lower than estimates from studies elsewhere (Table 1); much higher densities were documented in the Kenai National Wildlife Refuge, Alaska (Smith 1981), east central Saskatchewan (Fox et al. 1980, Yonge 1981), and parts of central Minnesota (McIntyre 1978, Titus and VanDruff 1981). In fact, our estimate is most similar to densities from the northeastern U.S., an area known for extremely low densities of loons (McIntyre 1988). Competition with Pacific Loons for breeding sites may be limiting the number of Common Loons on the Yukon Flats. Densities of Red-throated Loons were much lower than densities of Pacific or Common Loons throughout Alaska. This trend was even more evident in our study, where the paucity of sightings prevented the calculation of a density. This is not unexpected however, since Red-throated Loons are found in proportionately greater numbers in coastal areas (McIntyre, pers. comm.).

Accurate comparisons among studies were hampered by differences in geography, survey methodology, habitat type, and status of loons (Table 1). Ground surveys consistently yielded higher estimates than aerial surveys. Visibility bias associated with aerial surveys may account for some difference (Caughley 1977: 35), especially if the survey methodology does not sufficiently correct for bias. Smith (1981) and McIntyre (in prep.) tried to eliminate visibility bias by circling lakes repeatedly. This may prove costly, however, if a large area is to be surveyed, and would be logistically difficult in areas with complex lake systems. Lower densities may also result because aerial surveys cover much broader geographic regions than ground studies, and as a result, may include large areas of poorer quality habitat.

The habitat type used for calculating densities also confounded comparisons of studies. Estimates based on water area alone were always higher than estimates based on land and water. Intuitively, combining land area with water for a density estimate of a hydrophilic species reduces the final density. However, comparing densities across habitat types is not always possible; many researchers cannot determine the area of water surveyed (especially in transect studies) or fail to include the area of land and water surveyed.

Whether researchers count pairs, family groups, or nonbreeders also strongly affects estimates. Many times, the nature and timing of the study dictates what is counted. Generally, researchers studying breeding biology include only breeding individuals and derive a breeding pair or nesting density, whereas aerial surveyors include all loon sightings and derive a population density.

Finally, seasonal differences in loon visibility and abundance may influence estimates. For example, early summer surveys may miss incubating adults, but provide greater assurance that adults seen are on territories. Whereas, late summer surveys may include young of the year, and aggregations of failed and non-breeders.

Such factors must be considered for meaningful

TABLE 1. Density estimates (loons/km²) of Common, Pacific, and Red-throated loons from 17 studies in North America.[a]

Species and study area	Water		Land and water		Surveyed area (km²)	Survey type[b]	Time of survey[c]	Source
	Pair	All	Pair	All				
Common Loon								
Yukon Flats NWR, Alaska	—	—	—	0.12[d]	26,000.0	Ac	J	This study.
Kenai NWR, Alaska	—	9.35	—	—	155.0	A[e]	Ju-Au	Smith 1981.
East Central Saskatchewan	—	5.26	—	—	38.5	Gb	M-S	Fox et al. 1980
East Central Saskatchewan	4.79	4.83	—	—	41.2	Gb	M-S	Yonge 1981.
East Central Alberta	0.58	—	—	—	114.3	Gb	M-Au	Vermeer 1973.
Whitefish Lakes, Minnesota	0.95	1.15	—	—	46.6	Gb	A-Au?	Valley 1987.
Knife Lake Area, Minnesota	—	—	0.67	—	155.4	Gb	M-O	Olson & Marshall 1952.
Knife Lake Area, Minnesota	—	2.85	0.89	0.92	165.0[f]	Gs	M-Au	Titus & VanDruff 1981.
Itasca State Park, Minnesota	—	5.50	—	—	11.0	Gb	J	McIntyre 1978.
Maine, New Hampshire	0.36	—	—	—	252.2	Gb	M-J	Strong et al. 1987.
New York	0.59	—	—	—	282.3[g]	Gb	M-Au	Trivelpiece et al. 1979.
Pacific Loon								
Arctic Coastal Plain (ACP), Alaska	—	—	—	0.38	68,218.0	A	J-Ju	King, unpubl.[h]
National Petroleum Res. (NPR), within ACP	—	—	—	0.75	42,000.0	Ac	Ju-S	King 1979.
Storkensen Point, within NPR	—	—	—	1.59	18.0	Gs	J-Au	McDonald & Kenyon, unpubl.
Storkensen Point, within NPR	—	—	—	1.60	7.8	Gs	J-Au	Bergman & Derksen 1977.
Yukon Flats NWR, Alaska	—	—	—	0.49	26,000.0	Ac	J	This study.
Yukon-Kuskokwin Delta, Alaska	—	—	6.42	—	12.3	Gb	M-Au	Petersen 1976.
McConnell River, NWT, Canada	—	—	4.24	—	16.5	Gb	M-Au	Davis 1972.
Red-throated Loon								
ACP, Alaska	—	—	—	0.04	68,218.0	A	J-Ju	King, unpubl.[h]
NPR, within ACP	—	—	—	0.10	42,000.0	Ac	Ju-S	King 1979.
Storkensen Point, within NPR	—	—	—	0.57	18.0	Gs	J-Au	McDonald & Kenyon, unpubl..
Storkensen Point, within NPR	—	—	—	1.40	7.8	Gs	J-Au	Bergman & Derksen 1977.
Yukon-Kuskokwin Delta, Alaska	—	—	0.49	—	12.3	Gb	M-Au	Petersen 1976.
McConnell River, NWT, Canada	—	—	4.73	—	16.5	Gb	M-Au	Davis 1972.

[a] Density estimates calculated for the area of open water (Water) or land and water combined (Land & Water); "Pair" refers to the number of paired individuals (breeding or not); "All" refers to the number of paired and single loons.
[b] Ac: aerial survey with correction factor; A: aerial survey without correction factor; Gs: ground survey; Gb: ground breeding biology study.
[c] A: April; M: May; J: June; Ju: July; Au: August; S: September; O: October; ?: information not presented in publication.
[d] Density estimate may be unreliable due to low sample size ($n = 24$).
[e] Ground counts on 20 lakes indicated aerial counts needed no correction factors.
[f] Surveyed area includes land and water.
[g] Value represents average study area size; actual area surveyed was 172.5 km² in 1977 and 392.1 km² in 1978.
[h] Average values for 1986–1990, estimate assumes all loons were observed.

comparisons of studies. We recommend the implementation of a standard survey approach to enhance comparisons. In areas where loons and people exist in close proximity, using volunteers to monitor loons may be the best. The survey costs little and many people develop a greater appreciation for loons.

In large, remote areas, aerial surveys are the only pragmatic solution for estimating population densities. The aerial line transect methodology, used in this study, offers the advantage of automatically correcting for visibility bias (Quang and Lanctot 1991) and allows quick and relatively inexpensive coverage of large areas. The method is easy to repeat, which allows population trends to be determined over time. The calculated density estimates may be conservative, however, since some of the assumptions of the model may not be met (e.g., 100% detection of loons at a line parallel to the flight path; see Quang and Lanctot 1991).

The methodology is also affected by the propensity of loons to dive, the number of loon species in the area, and whether pre-fledged young are counted. These three factors (and possibly others) dictate the speed and altitude of the survey flight. A fast speed (167 km/hr or 90 knots/hr) and an altitude of 60 to 75 m may be best to observe loons before they dive. Where more than one loon species exists or when pre-fledged young are counted, flying slower and/or at lower altitudes may be necessary to accurately identify individuals at the expense of not identifying loons that dive too quickly.

More specific recommendations are difficult because of the diversity of questions being addressed by the many different natural resource organizations. Strong (1990) suggests that surveys be conducted when pre-fledged young are present; this provides information on productivity, a potentially more useful index than numbers of adults. Regardless of the methodology used, we do recommend reports include as much information as possible (e.g., number and status of counted loons, timing of survey, surveyed habitat type and area) for accurate comparisons.

The North American Loon Fund provided financial support for flying, and the Yukon Flats National Wildlife Refuge and the Alaska Fish and Wildlife Research Center provided logistical support. M. Vivion was instrumental in developing the project and piloting the aircraft. J. Jansen and R. Lanctot were passenger-observers during the survey. Data from unpublished reports by R. C. Kenyon, R. J. King, and D. McDonald are thankfully acknowledged. We also thank R. E. Gill, Jr., J. W. McIntyre, M. E. Petersen, L. Slater, N. Tankersley, and two anonymous reviewers for providing criticism on an earlier draft of this manuscript.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check list of North American birds. 6th ed. Allen Press, Lawrence, KS.

BERGMAN, R. D., AND D. V. DERKSEN. 1977. Observations on Arctic and Red-throated Loons at Storkersen Point, Alaska. Arctic 30:41–51.

CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, Inc., New York.

DAVIS, R. A. 1972. A comparative study of the use of habitat by Arctic Loons and Red-throated Loons. Ph.D.diss., Univ. of Western Ontario, London, Ontario, Canada.

FOX, G. A., K. S. YONGE, AND S. G. SEALY. 1980. Breeding performance, pollutant burden and eggshell thinning in Common Loons *Gavia immer* nesting on a boreal forest lake. Ornis Scand. 11: 243–248.

KING, R. J. 1979. Loon abundance and distribution in the National Petroleum Reserve—Alaska (NPR-A). Pacific Seabird Group 6:41.

LEE, M., AND J. ARBUCKLE. 1988. Maine Common Loons: a glance back and an eye toward the future, p. 167–176. *In* P. I. V. Strong [ed.], Papers from the 1987 conference on loon research and management. North American Loon Fund, Meredith, New Hampshire.

MCINTYRE, J. W. 1978. The Common Loon: Part III. Population in Itasca State Park, Minnesota 1957–1976. Loon 50:38–44.

MCINTYRE, J. W. 1986. Common Loon, p. 679–695. *In* R. L. Di Silvestro [ed.], Audubon Wildlife Report 1986. Natl. Audubon Soc., New York.

MCINTYRE, J. W. 1988. The Common Loon. Spirit of northern lakes. Univ. of Minnesota Press, Minneapolis.

MCNICHOLL, M. K. 1988. Common Loon distribution and conservation problems in Canada, p. 196–214. *In* P. I. V. Strong [ed.], Papers from the 1987 conference on loon research and management. North American Loon Fund, Meredith, New Hampshire.

MUNRO, J. A. 1945. Observations of the loon in the Cariboo Parklands, British Columbia. Auk 62:38–49.

NORTH, M. R. 1986. Breeding biology of Yellow-billed Loons on the Colville River Delta, arctic Alaska. M.S.thesis, North Dakota State Univ., Fargo, N.D.

OLSON, S. T., AND W. H. MARSHALL. 1952. The Common Loon in Minnesota. Univ. of Minnesota Press, Minneapolis.

PETERSEN, M. R. 1976. Breeding biology of Arctic and Red-throated Loons. M.S.thesis, Univ. of Calif., Davis, CA.

PETERSEN, M. R. 1979. Nesting ecology of Arctic Loons. Wilson Bull. 91:608–617.

QUANG, P. X., AND R. B. LANCTOT. 1991. A line transect model for aerial surveys. Biometrics 47: 1089–1102.

SJÖLANDER, S., AND G. ÅGREN. 1976. Reproductive behavior of the Yellow-billed Loon, *Gavia adamsii*. Condor 78:454–463.

SMIT, C., K. RAPPOLDT, AND M. KERSTEN. 1981. On the accuracy of shorebird counts over de Nauwkeurigheid van Wadvogeltellingen. Limosa 54:37–46.

SMITH, E. L. 1981. Effects of canoeing on Common Loon production and survival on the Kenai National Wildlife Refuge, Alaska. M.S.thesis, Colorado State Univ., Fort Collins, CO.

STRONG, P. I. V. [ED.]. 1988. Papers from the 1987 conference on loon research and management. North American Loon Fund, Meredith, New Hampshire.

STRONG, P. I. V. 1990. The suitability of the Common Loon as an indicator species. Wildl. Soc. Bull. 18:257–261.

STRONG, P. I. V., J. A. BISSONETTE, AND J. S. FAIR. 1987. Reuse of nesting and nursery areas by Common Loons. J. Wildl. Manage. 51:123–127.

SUTCLIFFE, S. A. [ED.]. 1979. The Common Loon: proceedings of the second North American conference on Common Loon research and management. Natl. Audubon Soc., New York.

TITUS, J. R., AND L. W. VANDRUFF. 1981. Response of the Common Loon to recreational pressure in the Boundary Waters Canoe Area, northeastern Minnesota. Wildl. Monogr. No. 79.

TRIVELPIECE, W., S. BROWN, A. HICKS, R. FEKETE, AND N. J. VOLKMAN. 1979. An analysis of the distribution and reproductive success of the Common Loon in the Adirondack Park, New York, p. 45–56. *In* S. Sutcliffe [ed.], The Common Loon: proceedings of the second North American conference on Common Loon research and management. Natl. Audubon Soc., New York.

U.S. FISH AND WILDLIFE SERVICE. 1987. Yukon Flats National Wildlife Refuge: comprehensive conservation plan, environmental impact statement, and wilderness review. U.S. Fish Wildl. Serv. Report, Anchorage, AK.

VALLEY, P. 1987. Common Loon productivity and nesting requirements on the Whitefish Chain of Lakes in north-central Minnesota. Loon 59:3–11.

VERMEER, K. 1973. Some aspects of the nesting requirements of Common Loons in Alberta. Wilson Bull. 85:429–435.

YONGE, K. S. 1981. The breeding cycle and annual production of the Common Loon (*Gavia immer*) in the boreal forest region. M.S.thesis, Univ. of Manitoba, Winnipeg, Manitoba, Canada.

The Condor 94:286–289

NESTING DENSITY AND COMMUNAL BREEDING IN AMERICAN OYSTERCATCHERS[1]

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Key words: Communal breeding; polygyny; American Oystercatchers; Haematopus palliatus.

American Oystercatchers (*Haematopus palliatus*) are typically monogamous shorebirds. The two sexes exhibit highly synchronized behavior during the period when females are susceptible to extra-pair copulations; they have stable, highly complementary pair bonds over many years; they have low divorce rates (about 2.5%, Nol, pers. observ.); and the care of both parents appears to be required for successful reproduction (Nol 1985).

One case of communal breeding involving two pairs attending and defending one communal nest has been reported for American Oystercatchers nesting along the Texas coast (Chapman 1982). Little is known regarding the ecological conditions in this study. Unlike most birds that breed communally (Fry 1972, Brown 1974, Brown 1987), some populations of American Oystercatchers are migratory and breed in a seasonal environment. Here, we document several cases of communal breeding in American Oystercatchers and the ecological conditions that appear to influence the occurrence of this unusual social system.

STUDY AREAS AND METHODS

We compared two breeding populations of oystercatchers. In Virginia, American Oystercatchers bred on Wallops and Assawoman Islands and were studied from 1978 to 1983. We include in the study, those breeding around the Chincoteague Channel (37°55′N, 75°23′W) from 1981 to 1983. In Virginia, pairs nested on sand habitat at the ocean side of the barrier island between the dunes and the high tide line, and in the salt marsh on elevated sandy dredge soil. Each year the number of nesting pairs was recorded. At the end of the study, aerial photographs (dated from 1982) were used to determine the area of nesting habitat available within the study site. Available habitat was defined as any habitat that had been used by nesting oystercatchers during the study period. We calculated the nest densities as the number of pairs on a given area. Clutch sizes ranged from two to four eggs ($\bar{x} = 2.24$ eggs for 294 nests, Nol et al. 1984).

In New York, we studied a population in the salt marshes around South Oyster Bay (40°38′N, 73°28′W) and Great South Bay (40°36′N, 73°20′W), Long Island, from 1983–1985 and 1987–1988. Oystercatchers bred in this region until the turn of the century, when hunting pressure presumably drove them southward (Bent

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