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Survival of Adult Red-throated Loons (*Gavia stellata*) May be Linked to Marine Conditions

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Abstract.—Large variations in the summering population size of Red-throated Loons (*Gavia stellata*) have occurred in recent decades in Alaska. Little information exists about annual or seasonal survival rates of adult Red-throated Loons. This study used tracking data from satellite transmitters implanted into 33 Red-throated Loons captured on breeding areas in Alaska to estimate annual survival with the sampling effort split between two study periods: 2000-2002 and 2008-2010. Mortality was inferred from transmitted sensor data that indicated body temperature of the Red-throated Loon and voltage of the transmitter's battery. Two definitive mortalities occurred, resulting in an annual survival estimate of 0.920 (SE = 0.054). The fates of two additional Red-throated Loons were ambiguous and, when treated as mortalities, the annual survival estimate was 0.838 (SE = 0.074). All four putative mortalities occurred during the non-breeding season in the early study period. Oceanic conditions, indexed by the Pacific Decadal Oscillation, appeared to differ between the study periods with higher Pacific Decadal Oscillation values associated with the early study period. Given that high values for Pacific Decadal Oscillation were also associated with the large decline of Red-throated Loons observed in Alaska during 1977-1993, this study suggests that survival of adult Red-throated Loons may vary in relation to the state of the marine ecosystem and thus contribute to long-term variation in population trends. *Received 30 January 2013, accepted 26 April 2013.*

Key words.—bycatch, *Gavia stellata*, mortality, Pacific Decadal Oscillation, Red-throated Loon, satellite telemetry.

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Red-throated Loons (*Gavia stellata*) breed in low densities throughout the circumpolar Arctic and, to a lesser degree, in taiga habitats (Groves *et al.* 1996; Gibbons *et al.* 1997; Hodges and Eldridge 2001). Annual aerial surveys across most major wetlands in Alaska identified a steep decline in numbers of Red-throated Loons from 1977 to 1993 (Groves *et al.* 1996), thereby identifying the species as one of conservation concern (McCaffery 2000). However, more recent surveys have indicated an increase in Alaska (Mallek and Groves 2009). Similarly, in Britain, Red-throated Loons declined between national surveys in 1983 and 1994, but then increased by the time of the next national survey in 2006 (Dillon *et al.* 2009). To enable identification of the ecological factors affecting population trends, estimates of key demographic rates (Sæther and Bakke 2000), such as productivity (e.g., number of fledged young per breeding pair) and adult survival, are needed. Several studies have examined productivity of Red-throated Loons (Gomersall 1986; Douglas and Reimchen 1988; Eberl and Picman 1993; Ball 2004), but there have been no studies of adult survival for Red-throated Loons.

The life history of loons (Order Gaviformes) is generally similar to seabirds, which is characterized by relatively high and invariant survival of adults (Schmutz 2009). The only published studies of adult survival in the genus *Gavia* are those by Nilsson (1977), who studied Arctic Loon (*G. arctica*) in Europe (point estimate of 0.89), and Mitro *et al.* (2008) who studied Common Loon (*G. immer*) in eastern North America (point estimate of 0.91). Their estimates conform to the seabird pattern, though their ability to examine variability in survival was limited. One might expect *a priori* a similarly high rate of survival for adult Red-throated Loons. However, Red-throated Loons are the smallest *Gavia* species as well as the oldest and most phylogenetically distinct within Gaviformes (Lindsay 2002), thus raising the possibility of a different life history. Red-throated Loons are also the most marine dependent species in Gaviformes, exploiting coastal marine prey during all months of the year. Other avian piscivores reliant on marine ecosystems (e.g., Black-legged Kittiwakes, *Rissa tridactyla*) show evidence of disparate survival among marine ecosystems in relation to disparate patterns of ecosystem

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productivity (Coulson 2002; Frederiksen *et al.* 2005). Thus, ecosystem shifts in productivity, indicated by climatic indices such as the Pacific Decadal Oscillation (PDO; Mantua and Hare 2002), may influence survival of Red-throated Loons.

Acquiring survival data for Red-throated Loons is difficult because they occur in low densities, and external markers (e.g., color bands) are best applied to the tarsi, which are usually under the waterline, rendering such markers difficult to observe. Further, their dispersed distribution on marine waters outside the breeding season limits mark-resighting work to just the breeding season (e.g., Mitro *et al.* 2008) and thus provides no ability to examine seasonal patterns of survival. Implantable satellite transmitters (Platform Transmitter Terminals, or PTTs) provide a means to obtain survival data year round. They likely incur less hydrodynamic drag than external transmitters (Pennycuick *et al.* 2012), and a recent study identified that implanted devices have fewer impacts on marine animals than external devices (White *et al.* 2013). Survival rates of Canada Geese (*Branta canadensis*) implanted with PTTs were similar to those for geese without PTTs (Hupp *et al.* 2006, 2008), suggesting that unbiased survival data for Red-throated Loons can be obtained with these techniques. This study quantifies survival of adult Red-throated Loons breeding in Alaska using PTTs implanted during two time periods: 2000-2002 and 2008-2010.

METHODS

Study Area

Red-throated Loons were captured at four study sites, encompassing all the major breeding areas for the species in Alaska (Groves *et al.* 1996). From south to north, these areas were the Copper River Delta (60.4° N, 145.4° W), the Yukon-Kuskokwim Delta (61.2° N, 165.1° W), the northern Seward Peninsula (66.6° N, 163.7° W), and the Arctic coastal plain (70.4° N, 150.7° W).

Adult Red-throated Loons were captured while resident on breeding ponds. Most Red-throated Loons were captured using a bow trap (n = 28) while they incubated on nests (Salyer 1962). Some Red-throated Loons (n = 10) were captured while tending chicks by deploying mist nets near chicks on breeding ponds. Once captured, a Red-throated Loon was placed inside a small, padded portable dog kennel and then transported (5-30 min) to a field surgery site. Sterile surgical procedures were used to implant satellite transmitters into the abdominal cavity with an antenna protruding out of the body (Korschgen *et al.* 1996). This surgical procedure, codified as a Standard Operating Procedure by the U.S. Geological Survey Alaska Science Center, was similarly performed each year of our study. The same anesthetic (propofol) was used during all surgeries. Red-throated Loons were released back to nesting lakes within 3 hr of capture. Any Red-throated Loons that died within the 2 weeks following surgery (n = 5; 13%) were removed from the survival analysis, attributing such mortality to the surgical process (Mulcahy and Esler 1999). One of these five deaths was of a bird caught while tending young; the other four were birds captured while incubating nests. Estimation of survival was based on the remaining 33 PTTs. These 33 PTTs were deployed across a series of years: 12 in 2000, 11 in 2001, 1 in 2002, 3 in 2008, 2 in 2009, and 4 in 2010. I refer to 2000-2002 (n = 24) as the early study period and 2008-2010 (n = 9) as the later study period.

PTTs were programmed with a duty cycle to emit signals for 8 hr at a time, followed by a quiescent period ranging from 48 to 108 hr, depending on the season and year. The Argos satellite system (Douglas *et al.* 2012) received signals. In addition to location estimates, data sent to the author from Argos included temperature (thus indicating whether the Red-throated Loon was alive or dead) and battery voltage. Mortality was inferred if temperature declined while battery voltage remained stable. If voltage declined while the temperature remained stable, the Red-throated Loon was inferred to be alive, and data were censored once a steep voltage decline induced variable or no temperature data. If both voltage and temperature were stable throughout a PTT's transmission history, the Red-throated Loon was inferred to be alive and data were censored at the time of signal loss. Two occasions of such signal loss were subsequently followed by resighting of the PTT-marked Red-throated Loons (via color bands that were applied to some; J. A. Schmutz, unpubl. data), confirming that transmitter failure occurred and therefore censoring was appropriate. For two PTTs, voltage decline and temperature decline were concurrent, causing ambiguity in whether mortality occurred. Thus, the survival analysis was done twice, once treating these ambiguities as deaths and once treating them as surviving and then censored.

I used the nest survival model type in program MARK (White and Burnham 1999) to estimate survival of adult Red-throated Loons. This model type is a flexible maximum likelihood approach to the Mayfield method for nest survival analysis and is described in detail by Dinsmore *et al.* (2002). This approach is useful when the entry and exit of individuals in the analysis are asynchronously staggered over time. I binned data for each half-month period, resulting in 24 periods per year in which Red-throated Loons were categorized as alive, dead, or censored. Given the relatively small

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sample size of PTTs and few deaths, simpler models with fewer parameters were needed. I considered four seasonal periods: summer (June-August), fall (September-December), winter (January-March), and spring (April-May). Note that these periods are not all the same duration of time; they are defined in relation to the typical migration chronology of the species, as discerned by the geographical analysis of these PTT data (J. A. Schmutz, unpubl. data). Summer and winter periods are times of relative stasis, whereas fall and spring are migratory periods. Red-throated Loons are slow migrants, and the fall migratory period for Red-throated Loons is particularly extended as they usually undergo a simultaneous molt of their flight feathers during that time (Barr *et al.* 2000).

I constructed seven different models to reflect various alternatives of how one might expect survival of Red-throated Loons to vary. The first two have been mentioned: a model with 24 parameters, reflecting half-month periods and with years pooled, and a model with four parameters—one for each season—with years pooled. I also constructed four models with just two parameters each. The seventh model was a one-parameter model (i.e., a null model with no variation).

The four models that each contained two parameters reflected various ecologically plausible hypotheses for how variation in survival of Red-throated Loons may occur: 1) breeding vs. non-breeding periods, given the unique costs and risks of reproduction (Erikstad *et al.* 1998; Golet *et al.* 2004); 2) migration vs. non-migration periods, as migration costs are significant, particularly for large birds (Klaassen 1996); 3) breeding and molt costs (Guillemette *et al.* 2007) vs. other periods without these costs, as these costs may outweigh migration costs; and 4) early vs. later study period, given that the earlier period occurred during the low point of population abundance and the later period was during a period of increase (Groves *et al.* 1996; Mallek and Groves 2009), which may correspond to changes in oceanographic conditions (Overland *et al.* 2008). The Akaike Information Criterion corrected for small sample size (AIC_c) was used to identify which models best represented the data (the lowest AIC_c; Burnham and Anderson 2002). AIC_c weights facilitated comparison of model fit between analyses that included vs. excluded ambiguous mortalities.

RESULTS

I received signals from PTTs for up to 15 months. The number of days that Red-throated Loons were known to be alive and available to die (i.e., exposure days; Dinsmore *et al.* 2002) was 8,801 with 5,501 occurring in the early years and 3,300 in the later years. Two definitive mortalities occurred in the early period during fall migration. Comparing the relative fit of competing models, a model with lower survival during migration seasons fits best, but closely competitive models were a null model of constant survival and a model with lower survival during the early study period (Table 1). The annual estimate of survival, given these two mortalities and constant survival, was 0.920 (SE = 0.054).

I reanalyzed the data after changing the status of two Red-throated Loons of ambiguous fate from censored to mortality, and thus a total of four mortalities in the data set. With these data, the annual estimate of survival was 0.838 (SE = 0.074). These two ambiguous mortalities both occurred in the early years with one occurring during fall migration and one during the winter season. Overall, the four mortalities in this analysis occurred in the early study period. Consequently, the best fitting model was the one that indicated survival was lower in the early study period than in the later period (Table 1).

Averaging the AIC_c model weights for these two versions of survival analysis yielded an AIC_c weight of 0.31 for the model with

Table 1. Seven different models of variation in the survival of adult Red-throated Loons marked in Alaska.

		Analysis with Two Mortalities		Analysis with Four Mortalities		Average of Two Analyses
Model of Survival Variation	Number of Parameters	ΔAIC_c	AIC_c weight	ΔAIC_c	AIC_c weight	AIC_c weight
Early vs. late years	2	0.60	0.194	0	0.439	0.317
Breeding vs. nonbreeding seasons	2	1.48	0.126	1.76	0.182	0.154
Invariant	1	0.52	0.203	1.86	0.173	0.188
Migration vs. non-migration seasons	2	0	0.263	3.06	0.095	0.179
Breed/molt vs. other seasons	2	0.95	0.164	3.76	0.067	0.115
All four seasons differ	4	3.31	0.050	4.62	0.043	0.047

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differing survival between study periods—approximately twice the magnitude as any other competing model (Table 1). When considering just a model with survival varying between early vs. late years and a model of constant (invariant) survival, and using weighted model averaging between data sets and between models, annual survival during the early study period was 0.833 (SE = 0.149) and during the later period it was 0.955 (SE = 0.071).

DISCUSSION

The annual estimate of survival of Red-throated Loons, when censoring birds of ambiguous fate, was 0.920, which is very similar to that of Common Loons (0.91; Mitro *et al.* 2008) and Arctic Loons (0.89; Nilsson 1977). Given that body size across species generally correlates with age at first reproduction (Western and Ssemakula 1982) and that Red-throated Loons weigh about 32% of Common Loons (Evers *et al.* 2010) and 55% of Arctic Loons (Russell 2002), one may expect that Red-throated Loons breed at an earlier age than other Gaviformes. A corollary of age of first breeding among species is adult survival rate, with early breeders having shorter lifespans (Sæther 1989). Little information exists about age of first breeding in Red-throated Loons, but Okill (1992) recaptured 11 breeding adults that were marked as chicks with age at first recapture as 4 years for males and 6 years for females. These data closely match the much larger data set for Common Loons (Evers *et al.* 2010). Given these similarities in age of breeding as well as consistent patterns among Gaviformes in clutch size investment (Russell 2002; Evers *et al.* 2010; J. A. Schmutz, unpubl. data), it seems logical that adult survival rates of Red-throated Loons may generally mirror their congeners despite body size differences.

Life histories characterized by high survival rates typically exhibit low variability in survival (Sæther and Bakke 2000; Schmutz 2009). Consequently, studies of the effects of environmental variation on demography typically focus on impacts on breeding success, which is much more sensitive to ecosystem changes than adult survival. Many studies of seabirds have documented large variations in breeding performance in relation to oceanographic conditions (Byrd *et al.* 2008; Ancona *et al.* 2011). More recently, studies have revealed that adult survival of seabirds in many populations, although less responsive than reproductive parameters, also exhibits variability in relation to broad scale changes in climate and related oceanographic states (Sandvik *et al.* 2005, 2012). This sensitivity of adult survival to marine conditions is relevant to Red-throated Loons as they are the most marine-associated of all Gaviformes. Long-term patterns of ocean climate in the North Pacific have exhibited decadal scale patterns of variability, sometimes referred to as regime shifts due to rather quick transitions between different mean climatic states, and are characterized by changes in currents and sea surface temperatures that then impart ecosystem changes through bottom-up effects (Mantua and Hare 2002). Overland *et al.* (2008) identified evidence of state changes in the PDO that correspond with long-term population variations in Red-throated Loons (Groves *et al.* 1996; Mallek and Groves 2009) with high PDO values occurring during the major period of population decline. Examining the PDO values (June to May) for the years of this survival study, the mean PDO value of the earlier years was -0.51 and that for the later years was -7.08. The difference in PDO value between these two study periods was 82% of the long-term (1900-2010) standard deviation of the PDO (Mantua and Hare 2002), thus suggesting an ecologically meaningful level of variability. These data on Red-throated Loon survival are too sparse to relate directly to oceanic conditions. However, the correspondence between low PDO values in the later study period with some empirical evidence of higher survival in the later study period (Table 1) raises speculation that adult survival in this species is affected by marine conditions.

In addition to evolved patterns of survival (Pfister 1998), anthropogenic effects on ecosystems can cause changes in both the mean

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and variance in survival (Schmutz 2009). Gillnets in marine systems often incur bycatch of seabirds, and diving piscivores such as loons (*Gavia* sp.) are particularly vulnerable (Žydelis *et al.* 2009; Warden 2010). One study of seabird bycatch in gillnets identified that 23% of all entangled birds were loons (*Gavia* sp.), which seems disproportionate to their abundance (Žydelis *et al.* 2006). It is unknown how Red-throated Loons in this study died as deaths were inferred from signals and not visually observed. There is a possibility that the actual survival rate for this study is lower than estimated if some Red-throated Loons that were censored were in fact mortalities caused by gillnets. Although this scenario is possible, it seems unlikely to be the major cause of censoring in this study. If indeed all censored Red-throated Loons in this analysis were gillnet mortalities, and the PTT-marked Red-throated Loons were not uniquely vulnerable to such mortality relative to other Red-throated Loons, then this would indicate that a substantial percentage of Red-throated Loons in Alaska are dying in nets. Such a result would be incongruous with the current increase in abundance of Red-throated Loons in Alaska (Mallek and Groves 2009). Instead, transmitter failure is the suspected cause for most censored Red-throated Loons in this study.

Annual survival of adult Red-throated Loons appears to be high. As with other species with high survival rates (Sæther and Bakke 2000), perturbations to Red-throated Loon survival are expected to have large impacts on population trends (Grear *et al.* 2009). Further study of survival is needed to enable reliable modeling of population responses to environmental variation. Evidence from a number of species of long-lived birds suggests that survival during non-breeding seasons constrains populations (Calvert *et al.* 2009). These limited data for Red-throated Loons also suggest most adult mortality occurs at this time of the year.

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