

3-4-2017

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Recommended Citation

Piper, W. H., Brunk, K. M., Flory, J. A., & Meyer, M. W. (2017). The Long Shadow of Senescence: Age Impacts Survival and Territory Defense in Loons. *Journal of Avian Biology*, n/a-n/a. <https://doi.org/10.1111/jav.01393>

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Piper, W. H., Brunk, K. M., Flory, J. A., & Meyer, M. W. (2017). The Long Shadow of Senescence: Age Impacts Survival and Territory Defense in Loons. *Journal of Avian Biology*, n/a-n/a. <https://doi.org/10.1111/jav.01393>

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The Long Shadow of Senescence: Age Impacts Survival and Territory Defense in Loons

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Decision date: 26-Feb-2017

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: [10.1111/jav.01393].

Abstract

Senescence, increased mortality that occurs among animals of advanced age, impacts behavior and ecology in many avian species. We investigated actuarial, reproductive, and behavioral senescence using capture, marking, and resighting data from a 26-year study of common loons (*Gavia immer*). Territorial residents of both sexes exhibited high annual survival (0.94) until their mid 20s, at which point survival fell to 0.76 and 0.77 in males and females, respectively. Sexual symmetry in actuarial senescence is somewhat surprising in this species, because males make a substantially greater investment in territory defense and chick-rearing and because males engage in lethal contests for territory ownership. Survival of displaced breeders (0.80) was lower than that of territorial residents in both young and old individuals. Old males and females also experienced slightly higher annual probability of eviction (0.16 for males; 0.17 for females) than prime-aged breeders (0.13 for both sexes), indicating senescence in territory defense. Prime-aged males reclaimed territories at a high rate (0.49), in contrast to females of the same age (0.33). However, old males resettled with success (0.35) similar to old females (0.31), suggesting that males decline in competitive ability as they age. Nonetheless males, but not females, showed an apparent increase in breeding success over the entire lifetime, a possible indication that very old males make a terminal investment in reproductive output at the cost of survival.

Introduction

Senescence is a decline in physiological function that occurs with advanced age (Monaghan et al. 2008). The exact cause of senescence is uncertain; however, it is thought to occur either because mortality reduces the number of individuals alive at old ages, weakening natural selection, (Hamilton 1966) or because of accumulated damage to living tissues from wear and tear over time (Ricklefs 1998).

Recent years have seen a substantial refinement in the measurement of senescence in wild populations. Workers now routinely distinguish between actuarial senescence, a decrease in annual survival rate that occurs in old individuals, and reproductive senescence, a decline in production of young that occurs among old individuals (Bouwhuis et al. 2012, Pardo et al. 2013). In addition, field biologists have begun to study many varied impacts that advanced age is likely to have on the physiology, ecology, and behavior of vertebrates, especially birds (Part et al. 1992, Hayward et al. 2013, Caudill et al. 2016).

One particularly rewarding outcome of recent studies has been the discovery of substantial differences between male and female senescence patterns. Since most birds are monogamous and exhibit biparental care, males and females should tend to make similar investments in reproduction (Owens and Bennett 1994, Liker and Székely 2005), a prediction borne out in many species (Frederiksen and Bregnballe 2000, Keller et al. 2008). However, polygynous or promiscuous species in which males invest heavily in male-male competition or mate attraction are likely to show early male senescence, since males are trading long-term survival for short-term reproductive success (Preston et al. 2011). Even monogamous birds are likely to exhibit asymmetry in senescence between the sexes, if one sex or the other invests disproportionately in parental care (Owens and Bennett 1994, Liker and Székely 2005).

Apart from its evolutionary significance, senescence has substantial ecological and behavioral impacts on avian populations. The weakening of older breeders creates opportunities for younger, healthier individuals to replace them, infusing an inherent dynamism into breeding populations (Reed et al. 2008, Sasvári and Hegyi 2011). Senescent animals, moreover, often show

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behavior distinct from that of young or prime-aged individuals. For example, old animals in some species make a terminal investment, working hard to maximize breeding success in their waning years at the cost of higher mortality (Part et al. 1992). Finally, senescence at the population level reduces production of young, which could make populations appear healthier than they are (Hitchcock and Gratto-Trevor 1997) and might even explain population cycles (Boonstra 1994).

Little is known about age-related changes in behavior and ecology of the common loon (*Gavia immer*), a large, charismatic, diving bird that breeds across much of northern North America. Common loons exhibit a rich, distinctive array of social behaviors likely to exhibit age-related variation. While loon pairs are monogamous (Piper et al. 1997), both sexes typically battle conspecifics to acquire and maintain ownership of territories (Piper et al. 2000). Males defend territories vocally via the territorial yodel, select the location for the nest (Piper et al. 2008b), provide more parental care (Jukkala and Piper 2015), and fight more dangerously than females (Piper et al. 2008a). Hence, though monogamous, loons exhibit a pronounced sex bias in territorial behavior and breeding investment that should lead to male-biased senescence.

We examined patterns of age-specific survival and territory acquisition in a marked population of common loons that has been under continuous study since 1991. Systematic efforts to mark and resight territorial individuals have made it possible to examine age-specific survival and behavior in this species (see Piper et al. 2000). One goal of our study was to describe actuarial, reproductive, and territorial senescence and determine if, as predicted, they are more severe in male loons. A second goal was to explore the possibility that the survival pattern seen in this species reflects lethal territorial battles that appear to occur chiefly in males (Piper et al. 2008a) and might represent a terminal investment by old males that aim to hold their territory for an additional year of breeding (see also Hall et al. 2009).

Apart from our interest in the evolution of senescence, our study has importance to the conservation of this charismatic species. A preliminary analysis (Mitro et al. 2008) reported a high rate of survival among territorial males and females, but that study followed breeders of unknown age over only a 10-year period and was blind to age-specific patterns in survival.

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Methods

Study animal

Common loons are migratory diving birds that breed chiefly across Canada and 14 northern United States, but also eastwards to Greenland and Iceland. The species winters along Pacific and Atlantic coasts of North America. Breeding pairs nest on shorelines, islands, emergent vegetation, logs, or boulders within freshwater lakes (Evers et al. 2010). Females lay two eggs, and joint incubation lasts 28 d. Parents feed and protect the one or two chicks until fledging, at about 11 weeks (Evers et al. 2010). Males produce the yodel, a loud territorial call (Walcott et al. 1999), which deters conspecific intrusion (Mager et al. 2007), and, during chick-rearing, reduces the likelihood that intruders will approach chicks (Jukkala and Piper 2015).

Study area

We investigated loon demography and behavior in a 900 km² study area in northern Wisconsin that includes central Oneida County (center: 45°42'N, 89°36'W) and adjacent portions of Vilas and Lincoln counties. Loons in this region reside on glacial lakes within northern hardwood and conifer forest; however, most study lakes have highly developed shorelines and experience heavy recreational pressure in the form of angling and boating. Loon territories comprise either entire small to medium-sized lakes (mean size ± SD: 55 ± 36 ha; N=96 pairs in 2016) or protected bays within large lakes (mean size ± SD: 358 ± 347 ha; N=29 pairs).

Capture, marking and sexing of loons

We spotlighted adult loons and their chicks at night and captured them in a 1.2 m diameter fishing net from the bow of a small motorboat (Evers 1993). Each captured loon was carried to shore, marked with a unique combination of a USGS metal band and three colored UV-resistant plastic leg bands (Gravoglas 2-Plex: GravoTech, Inc., Duluth, GA, U.S.A.), and released within 1 h. Through targeted efforts at capture, our marked study population grew steadily from an initial 4 pairs in 1991, and 45 pairs in 1996, to 125 pairs in 2016.

Resightings and detection of territorial eviction

Within two weeks of ice-out (mean date \pm SD = 15 April \pm 12d) each year, we made an initial visit to each loon territory to check identities of pair members from a canoe using 10 X 40 binoculars. After the initial visit, we returned at 4-6-day intervals to identify both pair members and record any nest or chicks. Final visits of the year occurred on August 7 or later, by which point most chicks were at least 6 weeks old. Almost all chick mortality occurs before six weeks of age (31 of 101 total chicks in 2016, 31%), rather than afterwards (3 of 101, 3%), so we regarded six-week-old chicks as having fledged.

One critical benefit of our systematic identification of pair members was detection of territorial eviction, which is the most frequent means of territory acquisition in loons of both sexes (Piper et al. 2000, Piper et al. 2015). Eviction occurs when a persistent intruder (always a “floater”: an adult that has not yet settled on territory or has lost one) engages in an escalating series of social behaviors with the same-sexed resident (see Sjölander and Ågren 1972) that culminates in a battle featuring both opponents standing upright in the water, grasping each other’s heads, and beating each other simultaneously with their wings until the resident becomes exhausted, flees, and deserts its territory (Piper et al. 2008a). Following eviction, displaced residents take refuge on adjacent lakes or bays (Piper et al. 2000) and become floaters, which intrude into the lake from which they were evicted and into neighboring lakes. Thus, evicted residents were typically resighted on or near their original lake or as intruders in lakes nearby. Regular “roving” observations were

made in June to non-study lakes in or on the periphery of the study area to find the few displaced residents not identified during routine observations.

Analysis of survival and territory loss/gain

We employed Program MARK (version 8.0), which uses maximum likelihood for survival analysis of marked animals, to analyze patterns of age-specific survival among loons (White and Burnham 1999). MARK uses an “encounter history”, a record of an animal’s “state” in each year across a fixed span of consecutive years, based on its year of marking and all subsequent resightings. Since we were interested in loss or gain of territory as well as survival, we conducted a multi-state analysis such that each loon could be identified for each year as a territory holder, a floater, or not observed. We included in our MARK analysis all male (N=197) or female loons (N=194) initially marked as territorial residents with chicks in the study area from 1991 through 2016. Pair members resighted in April on their original territory were assigned to the “T” state in the encounter history for that year; breeders whose position was usurped by another loon but were seen as intruders on that territory or elsewhere during the year were assigned to state “F” (for “floater”; Piper et al. 2000); individuals not observed during the year were assigned to state “0”.

The multi-state approach allowed us to model not merely apparent survival rate (Φ) and resighting rate (p), but also probability of transition (Ψ) between “T” and “F” states in both directions (Ψ_{TF} , Ψ_{FT}) by age and sex. Loons almost never desert a territory without immediately settling on another one (Piper et al. 2000). Instead, virtually all loss of territories comes about through eviction by another individual. Thus, the transition Ψ_{TF} reveals a loon’s capacity to hold its territory and allows us to measure the impact of age on susceptibility to eviction. Ψ_{FT} , on the other hand, indicates a loon’s capacity to settle on a second territory (or reclaim its original territory) after losing a first one. Since they could be examined across age-classes, apparent survival and transition probabilities had the potential to provide information about age-specific changes in mortality and

senescence. Finally, Program MARK's built-in capacity to account for resighting bias within each state made possible meaningful comparison of survival rates in floaters and territory holders.

Model selection and goodness of fit

As a preliminary step we tested the fully time-dependent model that MARK produced by default and inspected estimates of survival parameters by year. This permitted us to determine if some systematic pattern, such as cumulative degradation of habitat, might bias our estimates and obscure our results.

Following the test for a time-dependent pattern, we sought a general model that fit our data. Since we have recently shown age to have a substantial impact on behavior and body condition (Piper et al. 2015), we took as the general model one that included full age-dependence across classes of territorial status for Φ (apparent survival), and Ψ (both transitions). We assessed goodness of fit via the median \hat{c} procedure, which is appropriate when the general model is not fully time-dependent (Cooch and White 2006). We then used the computed median \hat{c} value to account for lack of fit of the general model and generate the quasi-likelihood-adjusted Akaike's information criterion, QAIC_c, accounting for small sample size (Burnham and Anderson 2002).

We sought a single best-fitting model (i.e. one that minimized QAIC_c) by systematically reducing the number of parameters (estimates of Φ , ρ , and Ψ by age- and sex-class) in the following sequence: resighting, apparent survival, and transitions. Owing to the many years of data, two sexes, and two states, there was a theoretically huge set of models to test. We pared down the list by recognizing that survival tends to be relatively stable among prime-aged breeding birds and then to decline in old individuals (e.g. Frederiksen and Bregnballe 2000, DuVal 2011). Thus we searched for a cut-off age at which optimal survival might cease and senescence begin, subject to the constraint that there be sufficient old age-classes to avoid sparse data. As a starting point, we estimated survival for the 1st through 15th age intervals collectively and placed together the 16th to 25th intervals as the older age-class. Next we systematically tested models that shifted this cut-off

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earlier or later by intervals of 2 years. We proceeded similarly in testing of parameters for transitions (Ψ_{TF} , Ψ_{FT}).

The chief goal of our MARK analysis was to produce estimates of annual probabilities for resighting, survival, and territorial transitions from the model that fit the data best through minimizing QAIC_c, or, if no model fit better than all others by 2 QAIC_c, using model-averaging to produce parameter estimates (Cooch and White 2006). Since parameter estimates for survival, resighting, and both transitions may be broken down by age-class and sex, comparison of parameter estimates reveals age- and sex-specific patterns for both survival and territory loss/gain.

Analysis of Age-specific Reproductive Success

To complement survival analysis via Program MARK, we investigated the possibility of reproductive senescence with our 26 years of breeding data. We analyzed males and females separately, because many details of their breeding and social behavior differ (Piper et al. 2008a, Jukkala and Piper 2015). As the dependent variable, we used number of fledglings produced each year (range of values: 0, 1, and 2) and conducted an ordered logit analysis (“ologit” command in STATA 14, College Station, TX). Since each bird-year was a separate observation in the analysis, most individuals contributed multiple records (maximum: 23), and standard errors were not independent. Hence, we performed repeated measures analysis (with clustered standard errors; “cluster” option in STATA). Long-lived birds typically show low reproductive success in their early years as breeders, which increases as they mature, and declines in later years (Weimerskirch 1992, McCleery et al. 2008, Reed et al. 2008), so we included both a quadratic term (age^2) and a linear one (age) as potential predictors of breeding success.

The analysis included both loons first banded on territory as unmarked, which were of unknown age (N=324), and loons banded as chicks that returned to settle, which were of known age (N=121). In order to combine these datasets, we assumed loons banded as adults were five years of age, if male, and seven years of age, if female, as recent data have shown (Piper et al.

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2015). However, we excluded the year of initial marking from our analysis, because our ability to capture adults only when they have chicks would have otherwise created a bias indicating that loons tend to produce chicks in their year of banding.

Data available from eCommons@cornell.edu via < <http://hdl.handle.net/1813/13098> >.

Results

Model-fitting and -averaging

There was no evidence of time-dependence in survival. Although estimated annual survival of territorial birds across all ages and both sexes fluctuated from a low of 0.88 ± 0.034 in 2013 to a high of 0.98 ± 0.021 in 2009, the full time dependent model fit the data poorly ($\Delta\text{QAIC}_c = 431$). Survival, moreover, showed no tendency to drift higher or lower during the study. Mean estimated survival was 0.938 from 1997-2008 and 0.936 from 2009 to 2016.

Our age-dependent general model produced a median c -hat of 1.82, indicating reasonably good fit to the data, so we adjusted models to produce QAIC_c values that accounted for this median c -hat and proceeded with model selection (Cooch and White 2006). Model selection produced ten models within 5 QAIC_c of the best model (Table 1). Hence, each of these models gained substantial support, and we carried out model-averaging to generate parameter estimates.

Resighting

All of the ten most parsimonious models called for resighting probability for territory holders to be estimated with a single parameter across all ages and both sexes ($p_{\text{terr}} = 1.0 \pm 0$); likewise all ten models used one parameter to estimate resighting probability for all floaters ($p_{\text{float}} = 0.707 \pm 0.026$).

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Apparent survival

All ten most parsimonious models estimated survival of territory holders separately for two age-classes: 1 to 17 and 18 to 25 years after capture; nine of these estimated male and female survival alike, while the 8th-ranked model used a separate parameter for males and females in the older age-class. Altering the most parsimonious model to estimate survival similarly across all ages of territory holders resulted in an increase of 9.5 QAIC_c, revealing that use of two age-classes improved the model greatly. Among floaters, all ten best-fitting models estimated survival similarly across all age-classes; the ninth best model used a separate parameter to estimate survival for males and females (Table 1).

Inspection of parameter estimates revealed that male and female territory holders survive at a high annual rate from one to 17 years after initial capture, whereas survival drops substantially in old territory holders of both sexes (Figs. 1, 2). Model-averaged parameter estimates for loons 1 to 17 years after banding were 0.94 ± 0.01 (SE) for both sexes, whereas apparent survival estimates for territory holders 18-25 years after banding were 0.76 ± 0.10 for males and 0.77 ± 0.07 for females. Using a mean settlement age of about 5 years (Piper et al. 2015), annual survival of adult males decreased by 19% from ages 5 - 23 to ages 24 and older. Based on a settlement age of 7 (Piper et al. 2015), female survival declines 18% between prime age, 7 to 25 years, and old age, 26 and older.

Floaters experienced apparent survival below that of prime-aged territory holders and similar to that of territory holders that had spent 18-25 y on territory (Fig. 2). The model-averaged estimate of survival was 0.80 ± 0.025 , 0.80 ± 0.034 , 0.80 ± 0.022 , and 0.80 ± 0.032 for 1-17 y males, 18-25 y males, 1-17 y females and 18-25 y females, respectively. Since all floaters had been banded initially as territory holders, floaters were also breeders that had been evicted from a previous territory (i.e. displaced breeders).

Loss of territory

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Five of ten best models used different parameters to estimate probability of territory loss for loons 1-17 versus 18-25 years on territory, four used the same parameter across year-classes, and one generated a separate estimate only for older females only (Table 1). Model-averaged probabilities of territory loss (\pm SE) were 0.13 ± 0.01 for both males and females with 1-17 years on territory and 0.16 ± 0.07 and 0.17 ± 0.07 , respectively, for males and females with 18-25 years on territory (Fig. 3). Hence, old loons of both sexes tended to lose their territories more often than did young loons.

Territory resettlement

The nine most parsimonious models all produced separate estimates for territory resettlement that differed between males 1 to 17 y after banding and all females; the tenth best model estimated resettlement rate identically across sexes and age-classes. In addition, three of ten best models used the same estimate for males of all ages. The importance of the sex difference in estimating parameters was confirmed by dropping it from the best overall model, which resulted in an increase of 3.7 QAIC_c. Model-averaging showed that about half of all male floaters are successful at reclaiming a territory annually from 1 to 17 years after initial capture (0.49 ± 0.06), but only about a third (0.35 ± 0.13) do so 18 to 25 years after banding (Fig. 3). Females showed little difference in territory resettlement with age, claiming a new territory at a rate of $0.33 (\pm 0.03)$ when young and $0.31 (\pm 0.08)$ when old (Fig. 3).

Reproductive senescence

Our separate analyses of age-specific fledgling production showed no dramatic increase or decrease with age (Fig. 4). The quadratic age term, which would have indicated a non-linear relationship, was not a significant predictor of breeding success in either males (coefficient = 0.00049 , $P=0.872$, $N=1400$ bird-yr among 244 loons) or females (coefficient = -0.0028 , $P=0.271$,

N=1203 bird-yrs among 201 loons), so it was dropped in both cases. The linear age predictor was marginally significant and positive in males ($r = 0.037$, $P < 0.02$), indicating an increase in fledglings produced with age (Fig. 4). Female breeding success showed a slight negative association with age, but it did not approach significance ($r = -0.012$, $P = 0.355$; Fig. 4).

Discussion

Actuarial senescence in males and females

Actuarial senescence is a conspicuous feature of loon demography. According to our analysis, both male and female loons enjoy a high rate of survival until about their mid 20s, at which point the mortality rate increases by roughly a factor of four. While sparse data in older age-classes prevented us from ascertaining the precise shape of the decline in survival, its extent appears comparable to that reported in other free-living birds (Bouwhuis et al. 2012, Pardo et al. 2013, Hammers et al. 2015).

Although later settlement by females (Piper et al. 2015) leaves open the possibility that females senesce at a slightly older age than males, actuarial senescence appears to be similar in timing and extent in male and female loons. In theory, sexual symmetry in actuarial senescence should occur when the sexes invest similarly in reproduction (Nussey et al. 2009, Preston et al. 2011). Female loons alone endure the energetic cost of egg production, of course, but males are 25% larger, produce the male-only territorial yodel to deter territorial intrusions, defend chicks more vigorously (Jukkala and Piper 2015), and are far more apt to participate in lethal contests for territory ownership (Piper et al. 2008a). Hence, males appear to make a greater reproductive investment, whether measured by territorial competition or rearing of young, yet suffer no penalty in terms of higher mortality.

Loss of competitive ability with age

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In contrast to the pattern in actuarial senescence, male loons, but not females, showed a steep decline in territory resettlement rate in their mid 20s. Males, in general, should resettle on a territory at a higher rate than females, owing to a female-biased adult sex ratio (Piper, unpublished data). Thus, males in the 1 to 17 y post-banding class show the expected inflated rate of resettlement, compared to females, while older males do not.

The cause of the low resettlement rate among old males is unclear. The pattern might arise because of an inability to compete effectively for a territory, drive off territorial intruders, maintain a pair bond, or engage in some other aspect of social or territorial behavior. But taken together with actuarial senescence and the slight uptick in vulnerability to eviction that impacts males in their mid 20s, reduced territory settlement in old males suggests a decline in some aspect of competitive behavior. Declines in competitive ability with age are well-known in birds (Arcese 1989, Kim et al. 2007) and mammals (Nussey et al. 2009, Pardo et al. 2013). As noted previously, earlier male senescence is expected in this species based upon males' greater investment in territory defense, dangerous territorial battles, and enhanced defense of offspring (Jukkala and Piper 2015).

The slight increase in vulnerability to territory eviction among older loons, evident in both sexes, shows that females too suffer a decrease in competitive ability with age that coincided with actuarial senescence. However, unlike males, females continue to resettle on vacant territories at a high rate despite old age. Senescence, therefore, is muted in females, as even those in the oldest age-classes maintain the capacity to reclaim territories at rates comparable to prime-aged females. As noted previously, this result is consistent with females' more limited investment in territory defense and breeding.

Apparent stability in breeding success among old males

While our findings suggest that old male loons retain substantial reproductive capacity, we must note two alternative hypotheses for this finding. First, the apparent stability of breeding

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success among old male loons might occur if a subset of males both survives longer than others and produces more offspring, thus biasing our sample of old males (Reid et al. 2003, Nussey et al. 2013). Only further study of individuals followed throughout life will allow us to test this possibility. Second, our finding might have resulted if old males offset declining body condition and competitive ability with greater reproductive experience. as DuVal (2011) reported in male lance-tailed manakins (*Chiroxiphia lanceolata*). While we have shown that male loons breed more successfully after their first few years on familiar territories by reusing nestsites where they hatched chicks in past years (Piper et al. 2008b), the steady increase in fledgling production reported here seems to continue well into the teen years (see Fig. 4), long after normal settlement age (4-7 years of age; see Fig. 1 in Piper et al. 2015). Hence, the apparent increased fledgling production among older males does not seem to result from improved site familiarity.

The apparent tendency of old male loons to fledge chicks at a rate similar to prime-aged males is surprising. Old males suffer declines in survival rate, capacity to resist eviction, territory resettlement, and body condition as they age (Piper et al. 2008a), so they would have been expected to suffer reduced breeding success, as seen in other long-lived birds (Sergio et al. 2011, Pardo et al. 2013). Old male loons might be able to maintain a high reproductive capacity throughout life by compensating for loss of competitive ability through increased investment in chick production. Since we have recently learned that older males show no increase in chick defense (Jukkala and Piper 2015), we presume that added investment by old males in chick survival might take the form of increased chick feeding or longer duration of parental care, both of which are currently being measured in our study population. If it comes at the cost of reduced energy spent on self-maintenance, such an increased investment in offspring by old males would constitute a terminal investment. Females show no loss in condition, a very mild decrease in competitive ability, and a possible slight loss in breeding success with age; hence they show no evidence of terminal investment.

Equal mortality among the sexes and fatal fighting

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Perhaps the most vexing conundrum posed by the equal actuarial senescence of males and females is that it is at odds with the fatal territorial battles reported in males (Piper et al. 2008a). Simply put, fatal male battles must produce a higher rate of male mortality at some point in the life history, so it is surprising to see little or no evidence of higher male mortality in any age-class we examined. Two points seem important to make here. First, while our analysis was effective at assessing survival patterns based on territory tenure (years spent on territory), we could not examine age *per se*. For instance, the class of territory holders in the first year post-banding contained a spectrum of individuals from young settlers (ages 4 to 8 years) to middle-aged (9 to 19 year-olds) to older individuals that had settled many years before we began to study them. Hence, our analysis inevitably blurred age-classes and missed fine age-based survival differences. Second, we had more robust data on territory holders than floaters, since all floaters measured were territory holders that had been evicted. Thus, we had limited ability to detect sex bias in survival of floaters. Fine-scale age-specific analysis of survival will be possible soon, as long-term marking of chicks has produced a growing sample of known-age adults of both sexes that are observed as floaters and on territory (Piper et al. 2015). This future analysis will pinpoint the stage of the life-history at which male mortality rate is high.

Survival of displaced breeders

Since floaters in our study were all displaced territory holders, our estimates of floater survival provide a preliminary window onto the survival of loons at this life history stage. Adult loons that have been evicted from a territory experience a decline in survival probability. There seem to be three explanations for this pattern. First, evicted loons might have suffered injury during eviction that reduces their prospects of survival. This explanation seems unlikely, as all loons that move from the territory holder to the floater state have succeeded in migrating to the wintering grounds, surviving a winter, and returning to the breeding grounds. Second, evicted birds might constitute a subset of all territorial birds in relatively poor condition and thus both likely to lose a battle for

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territory ownership and more likely to succumb to mortality during the year. Third, loons might alter their behavior following eviction in a way that negatively impacts survival, such as by fighting harder in an effort to regain a territory. We have insufficient data at present to distinguish between the second and third hypotheses.

Impact of vulnerability to eviction on nonbreeders seeking territories

The increased vulnerability of old breeders to eviction sheds light on a distinctive and puzzling aspect of territorial behavior: repeated visits by a young nonbreeder into an established territory. Recently we learned that nonbreeders do not establish competitive “footholds” by making many visits to a single territory and thus increasing their fighting ability on that specific territory (Piper et al. 2015). However, since territory holders lose competitive ability as they age, repeated visits to a single territory might permit a young nonbreeder to assess the condition of an ageing resident on the territory and to time an eviction attempt after the resident’s competitive ability has declined.

High survival of prime-aged loons; moderate senescence

Mitro et al. (2008) reported that common loons in both New England and northern Wisconsin survived with an annual probability of 0.92, based on a 10-year analysis of adults of unknown age. The limited duration of that analysis made it impossible to recognize more than one age-class. The use of a longer time interval and two age-classes allowed us a somewhat finer-scale picture of the loon population in Wisconsin. Our results suggest that adult loons may be split into a “prime-aged” class, which spans roughly ages 5 to 24 in males and 7 to 26 in females and survives at a probability of 0.94, and a much smaller, older age-class, in which the mortality rate has quadrupled to yield survival of 0.76 in males and 0.77 in females. Although some seabirds have higher rates (wandering albatross: *Diomedea exulans*; 0.97; Weimerskirch 1992, grey headed

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albatross: *Thalassarche chrysostoma*; 0.95 Prince et al. 1994), the survival probability of prime-aged loons is one of the highest reported among birds (Bouwhuis et al. 2012),

Acknowledgements – We thank C. Walcott and J. Mager for valuable field collaboration and countless research assistants for help with field observations, especially E. Andrews, F. Spilker, N. Banfield, K. Tischler, M. Klich, A. Reinke, M. Schwabenlander, A. Dolsen and E. Harrington. C. Brown assisted with Program MARK analysis. Funding was provided by National Science Foundation (IBN-0316442 and DEB-0717055), National Geographic Society, Disney Conservation Fund and Chapman University.

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Table Legend

Table 1. Ten best-fitting models found by Program MARK. Letters in the body of the table signify matching of parameter estimates within that model. For example, for the best-fitting model, a single parameter was used to estimate “S:terr ♂; 1-17” and “S:terr ♀; 1-17”, and a (different) single parameter also estimated all four classes of Ψ_{TF} .

S:terr ♂; 1-17	S:terr ♂; 18-25	S:terr ♀; 1-17	S:terr ♀; 18-25	S:float ♂	S:float ♀	p:terr	p:float	Ψ_{TF} ♂; 1-17	Ψ_{TF} ♂; 18-25	Ψ_{TF} ♀; 1-17	Ψ_{TF} ♀; 18-25	Ψ_{FT} ♂; 1-17	Ψ_{FT} ♂; 18-25	Ψ_{FT} ♀; 1-17	Ψ_{FT} ♀; 18-25	QAICc	Δ QAICc	AICc Weights	# parms	QDeviance
a	b	a	b	c	c	d	e	f	f	f	f	g	h	h	h	3278.2	0	0.2697	8	3262.1
a	b	a	b	c	c	d	e	f	g	f	g	h	i	i	i	3278.9	0.7071	0.1894	9	3260.8
a	b	a	b	c	c	d	e	f	f	f	f	g	g	h	h	3279.5	1.3048	0.1405	8	3263.4
a	b	a	b	c	c	d	e	f	g	f	g	h	h	i	i	3280.2	2.0182	0.0983	9	3262.1
a	b	a	b	c	c	d	e	f	f	f	f	g	h	i	j	3281.7	3.5640	0.0454	10	3261.7
a	b	a	b	c	c	d	e	f	g	f	g	h	i	j	k	3282.4	4.2649	0.0320	11	3260.4
a	b	a	b	c	c	d	e	f	f	f	g	h	i	j	k	3282.9	4.7146	0.0255	11	3260.8
a	b	a	c	d	d	e	f	g	h	g	h	i	j	k	l	3283.0	4.8852	0.0234	12	3259.0
a	b	a	b	c	d	e	f	g	h	g	h	i	j	k	l	3283.1	4.9297	0.0229	12	3259.0
a	b	a	b	c	c	d	e	f	f	f	f	g	g	g	g	3283.1	4.9805	0.0224	7	3269.1

Figure Legends

Figure 1

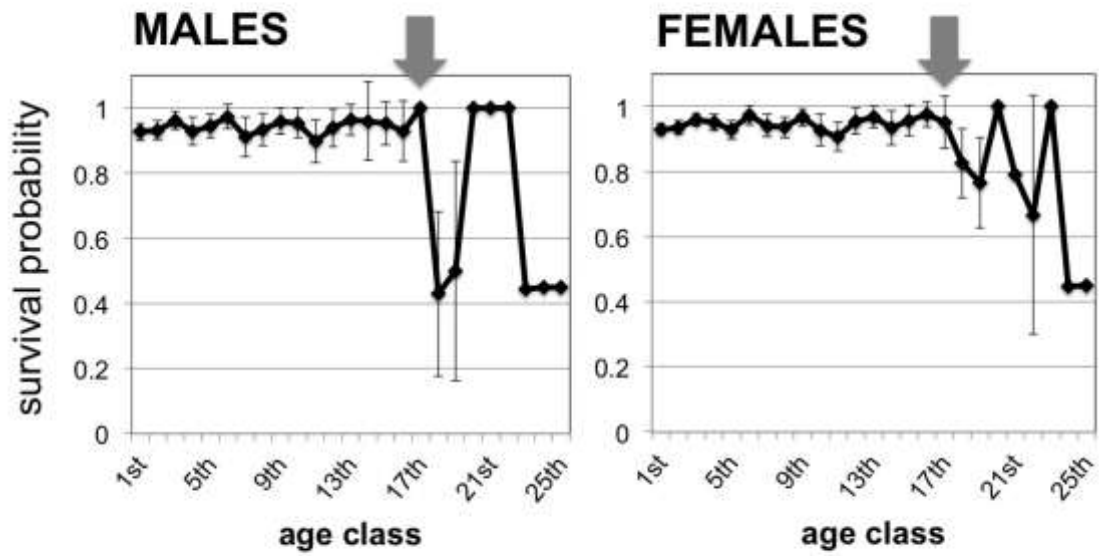


Figure 2

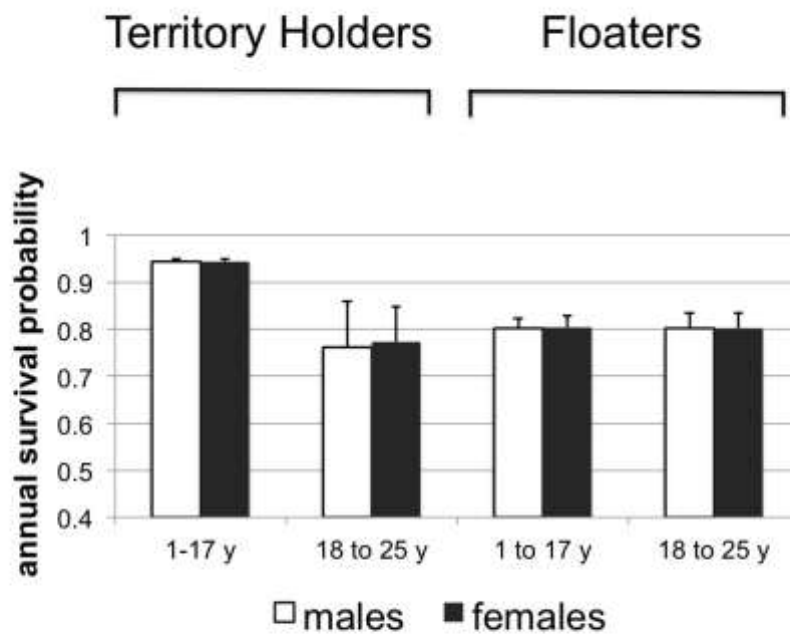


Figure 3

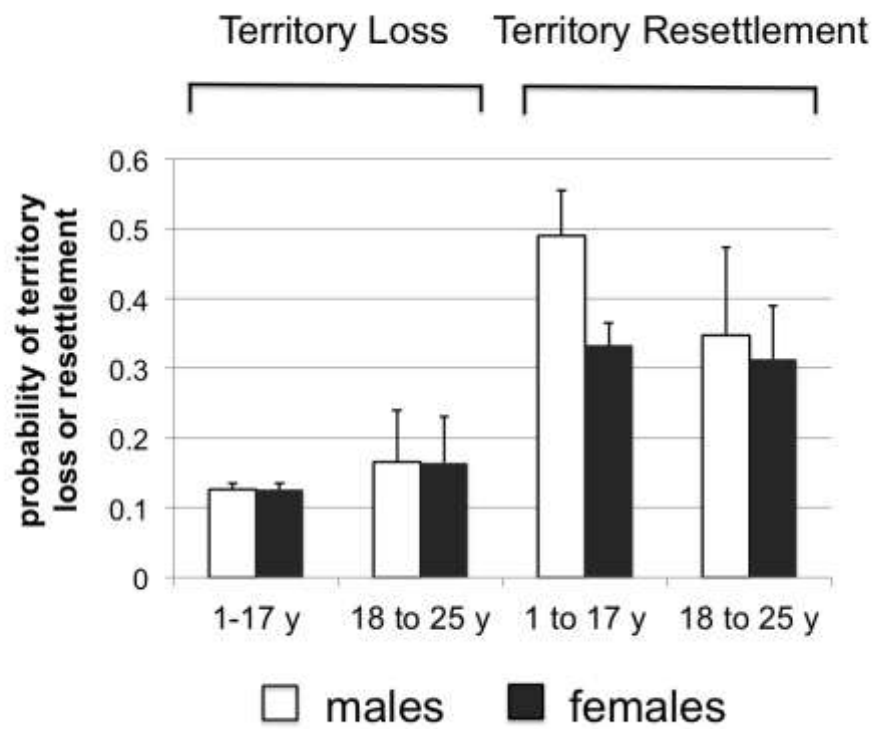


Figure 4

