



Aging male loons make a terminal investment in territory defense

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Received: 8 February 2018 / Revised: 11 May 2018 / Accepted: 15 May 2018 / Published online: 24 May 2018
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Abstract

Animals that senesce experience a decline in residual reproductive value (RRV), such that old individuals can expect reduced breeding success compared to young ones. According to life history theory, animals with low RRV, which thus have less to lose, should shift resources away from self-maintenance and towards reproduction, an expectation called terminal investment. In a population of common loons whose survival and territorial behavior were measured throughout life, males 14 years and older exhibited clear senescence, as they showed lower survival, reduced body mass, and far greater susceptibility to territorial eviction than younger males. While older males invested no more effort than young males in feeding or protecting their chicks, they increased territorial yodeling by 35%, showed more aggression towards territorial intruders, and, following eviction from original territories, resettled with great frequency on vacant, unproductive territories nearby. Our findings thus provide support for terminal investment in territorial behavior. Hyper-aggressive behavior by old, declining males might explain the unusual occurrence of lethal combat for territories in this species.

Significance statement

Life history theory holds that animals that decline with age should invest less energy in staying alive and more in reproduction when they become old, because they have less to lose in doing so. Evidence for such terminal investment, however, is scanty. We measured rates of survival and territorial behavior in a known-age population of common loons and found that males, but not females, suffered a decrease in survival rate and ability to hold a territory after age 14. At the same time, territorial males older than 14 behaved more aggressively and were more apt to give a territorial yodel call towards territorial intruders. Hence, our study appears a rare example of terminal investment in aggressive behavior, whereby old, declining males cling desperately to their territories in hopes of producing a few more offspring before they die.

Keywords Terminal investment · Aggression · Territory · Loon · *Gavia immer*

Introduction

Long-lived animals must balance the energetic demands of breeding and long-term survival (Hamilton 1966). The optimal balance between reproductive and somatic investment

depends, in part, upon details of the life history. In species that undergo senescence, a decline in physiological condition with age (Ricklefs 1998), old individuals can expect to produce fewer offspring than young individuals. The lower residual reproductive value (RRV) of old animals means they have less fitness to lose than young ones, which should spawn a “go for broke” strategy late in life: an increase in reproductive investment at the cost of somatic investment (Fisher 1930). The expectation of such a “terminal investment” in reproduction among senescing animals has been entrenched in the evolutionary literature for over 80 years (Fisher 1930; Pianka and Parker 1975; Clutton-Brock 1984).

Despite its enduring logic, evidence for terminal investment is limited. The smattering of reports of this phenomenon

Communicated by C. R. Brown

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is of two kinds. First, old individuals in a handful of species invest more heavily in provisioning of offspring (Pugesek 1981; Clutton-Brock 1984; Part et al. 1992; Descamps et al. 2007; Froy et al. 2013) or, in species lacking parental care, courtship (Felton et al. 2006; Ory et al. 2015). Second, some invertebrates and vertebrates show short-term increases in reproductive investment following experimental challenge to the immune system (Weil et al. 2006; González-Tokman et al. 2013; Bowers et al. 2015; Duffield et al. 2015). But these reports are exceptions; numerous studies have found no evidence for terminal investment in species that seemed prime candidates for the behavior pattern (e.g., Newton and Rothery 1997; Berube et al. 1999; Sergio et al. 2011; Hayward et al. 2013). Indeed, reviews have concluded that terminal investment is rare (Clutton-Brock 1984; Froy et al. 2013).

A partial explanation for the rarity of terminal investment might be the narrow focus of most studies that seek evidence for it. Most biologists have perceived that terminal investment is most likely to occur in breeding behavior per se, such as increased time spent courting mates, nourishing young, or keeping offspring safe from predators (Clutton-Brock 1984). But terminal investment could occur in any behavior that contributes to reproduction, directly or indirectly, such as settlement on or defense of a breeding space. Indeed, since it is often costly and dangerous, defense of a breeding territory is a behavior pattern that might be especially pronounced in individuals of low RRV (Pianka and Parker 1975; Clutton-Brock 1984). Of the few studies that have tried to detect indirect terminal investment of this kind, some have failed (e.g., Møller and Nielsen 2014; Kuczynski et al. 2015). Others have yielded evidence that is unclear or inconsistent. For example, Hall et al. (2009) reported that male wrens sang more territorial song in their last year of life, but found no correlation with age; Pugesek (1981) noted clear aggressive behavior which, however, might have constituted defense of young, not the territory per se.

The common loon (*Gavia immer*) is a monogamous, territorial species that affords an opportunity to investigate the possibility of terminal investment. Loons invest heavily in the breeding effort; both sexes contribute extensively to incubation and parental care (Evers et al. 2010). Detailed behavioral observation of a Wisconsin study population since 1993 has revealed that territorial eviction is the most common means by which nonbreeding adults acquire territories and that both male and female breeders must repel a ceaseless influx of nonbreeders bent on seizing their territorial position (Piper et al. 2000, 2015). The large sample of territory owners whose survival, condition, territorial status, and breeding behavior have been measured for up to 25 years (Piper et al. 2013) provides an opportunity to detect senescence and investigate the possibility of territorial behavior as a terminal investment.

Methods

Study area and reproduction of loons

We studied common loons in a roughly 2000 km² region in northern Wisconsin, USA, centered at 45° 42' N, 89° 36' W and which comprises most of Oneida County, together with portions of southern Vilas and northern Lincoln counties. This area contains about 200 glacial lakes used by loons, each bordered by northern hardwood and coniferous forest and used extensively for angling and boating. Breeding territories are occupied from April through October and consist mostly of entire small- to medium-sized lakes (mean size ± SD: 55 ± 36 ha; 96 pairs in 2016) but also a smaller number of protected bays within larger lakes (358 ± 347 ha; 29 pairs in 2016).

Common loons exhibit conspicuous black and white plumage during the breeding season but are sexually monochromatic. Males are 24% larger (mean mass ± SD = 4500 ± 310 g, *n* = 1070) than females (3630 ± 250 g; *n* = 914). Males select the nest location (Piper et al. 2008b), usually on an island or along a marshy or boggy shoreline, and females lay two eggs, incubated jointly by the pair for 28 days (Evers et al. 2010). Parents feed chicks most of their food through the first 6 weeks and continue to feed and defend them through week 11 (Evers et al. 2010).

Territory defense

Males and females must acquire a breeding territory in order to reproduce, either by evicting an established territory owner, replacing a dead one, or founding a new territory on a vacant lake (Piper et al. 2000). Territory holders seldom desert a territory (Piper et al. 2000); instead, they defend the territory from a parade of intruders seeking to evict them (Piper et al. 2006). At such times, males often emit the loud, complex yodel call, which discourages landing by flying nonbreeders (Mager et al. 2007). Aggression by male and female breeders towards intruders includes lunges, chases on the water's surface, and battles in which two opponents grasp each other's heads, beat each other repeatedly with their wings, and dunk each other's heads underwater (Piper et al. 2008a). While male evictions sometimes culminate in the death of the former resident, female battles rarely do (Piper et al. 2008a).

Marking and observation of loons

We captured adult loons and chicks by nocturnal spotlighting during July and August from 1993 to 2016 and fitted them with a USGS metal band and three plastic leg bands in unique combination (Gravoglas 2-Plex: GravoTech, Inc., Duluth, GA, USA). A drop of blood was taken from each chick for sexing (see Itoh et al. 2001). Adults and chicks were weighed and released in their territories.

On weekly visits between late April and early August, observers in canoes used 10×42 binoculars to identify all marked breeders and intruders from leg bands (which are visible at close range; during preening, resting, and flight; and may be seen briefly on many individuals as they dive), noted all nesting and chick-rearing behaviors, and recorded territorial intrusions. To measure chick attendance, observers conducted scan samples (Altmann 1974), recording distance between each adult and chick(s) (≤ 20 or > 20 m) at 5-min intervals. Finally, observers made note of all vocal and social behaviors, including territorial yodels by males and aggression.

Strictly speaking, observations were not performed blind, as we made no effort to make observers unaware of our goals and expectations. However, observers comprised 75 different individuals who conducted observations over a 24-year period during which research aims and techniques varied greatly. None was aware, for example, that an analysis of the age dependency of aggressive and territorial behavior would ultimately be carried out.

Analysis of senescence, territory loss, and territory resettlement

A recent analysis of successful breeders marked as adults revealed that many males and females survive into their mid-twenties (Piper et al. 2017), at which point both sexes senesce. But successful breeders are likely to be high quality individuals and thus might be expected to senesce at a later age than the overall population (see Sergio et al. 2011). In the present study, we examined senescence in a much broader cross-section of loons: those banded as chicks. This segment of individuals includes many that fail to fledge, others that perish on migration or during winter, and still others, termed adults banded as juveniles (“ABJs”), that return to the breeding grounds as adult floaters (adults that lack a territory) and attempt to breed.

Previous investigation of ABJs has shown important differences between the sexes that are likely to affect survival patterns and territorial behavior. For example, males exhibit short-distance natal dispersal ($10.2 \text{ km} \pm 6.6 \text{ SD}$, $n = 90$), and, if they settle, usually claim territories in our study area at 4 to 8 years of age (85 of 90 males; 94%). Females settle at between 5 and 9 years (Piper et al. 2015) and show long-range natal dispersal ($34.0 \text{ km} \pm 50.4 \text{ SD}$, $n = 41$). Males also exhibit an increase in body condition early in life that is lacking in females (Piper et al. 2015).

We analyzed demographic patterns among ABJ males and females (White and Burnham 1999) with Program MARK, running a separate MARK analysis for each sex owing to their differences in natal dispersal and life history. We used a multi-state model structure with three annual states (“T” for on territory, “F” for floaters, and “0” for not seen) that allowed us to model apparent survival rate ($\hat{\Phi}$), resighting rate (p), and

transitions between territory holder and floater states (Ψ_{TF} , Ψ_{FT}) from age zero to 18. Ψ_{TF} indicates a shift from territorial to floater status and, hence, territory loss; Ψ_{FT} signifies the shift from floater to territory holder, which indicates territory settlement among young loons or resettlement of older loons following territorial eviction.

Goodness of fit

Program MARK requires as an initial step that one find a relatively saturated general model that fits the data. In both males and females, age structure seemed likely to occur, as indicated by patterns in loon survival (Piper et al. 2017) and territorial behavior (Piper et al. 2015), and resightings of territory holders are consistently high. Accordingly, we selected as the general model in males one that had constant p for territory holders and had full age structure in all other parameters. This model yielded a c-hat value of 0.92 via the median c-hat procedure (Cooch and White 2006), indicating slight underdispersion for which we did not adjust (Cooch and White 2006). Among females, the general model held p and $\hat{\Phi}$ constant for territory holders, had minimal age structure for p and $\hat{\Phi}$ among floaters (intervals 1, 2, 3 and 4–18 estimated separately), and used full age structure for Ψ (Table 2). The median c-hat procedure produced a c-hat of 1.19 for this model, which was used to adjust model calculations and produce QAIC_c values (Burnham and Anderson 2002).

Previous knowledge of the loon system allowed us to fix certain known parameters in both models to avoid producing meaningless or inaccurate parameter estimates. Without exception, all territory holders are detected via multiple territory visits (nearly always on their territory from the previous year), so p_{terr} was fixed at one for both sexes. An earlier study estimated survival rates of young loons that do not return to the breeding grounds in large numbers; hence, $\hat{\Phi}_{\text{float}}$ was fixed at 0.77 for the first and second age intervals of both sexes (Piper et al. 2012). Finally, no young male floater has yet returned to the study area at age one, so p_{float} for the first age interval in males was fixed at zero.

Model selection

Our general approach to model selection was to produce configurations of parameters across age intervals that were plausible, given what we hypothesize or know about loon biology, and then test the importance of each age interval by comparing fit (based on AICc for males or QAICc for females) of models that included or excluded that age interval.

With p_{terr} , the resighting rate of territorial birds, fixed at one for all age intervals, we tested remaining model parameters in the sequence: p_{float} , $\hat{\Phi}_{\text{terr}}$, $\hat{\Phi}_{\text{float}}$, Ψ_{TF} , Ψ_{FT} . That is, we first optimized model fit (i.e., minimized AICc or QAICc) among parameters across age intervals for p_{float} , then did the same for

Φ_{terr} , and so on. We tested four separate age intervals for p_{float} (1, 2, 3, and 4–18) to accommodate known differences in rate of return among young loons of both sexes (Piper et al. 2015).

In looking for evidence of senescence, we selected the last five age intervals (i.e., 14–18) in both survival (Φ) and transition (Ψ) parameters as those (1) where senescence would be evident, if it occurred and (2) that together would provide a large enough sample so that senescence could be detected. Thus, the 14–18-year age interval was estimated separately for Φ_{terr} , Φ_{float} , Ψ_{TF} , and Ψ_{FT} .

Early age intervals were also added for testing when findings suggested patterns might exist in survival or territorial behavior. We added an additional age interval (interval 3) to Φ_{float} for female floaters to accommodate the somewhat later return of females to the breeding ground (Piper et al. 2015). Age structure for Ψ_{FT} included numerous early age intervals (males: 1–3, 4, 5, 6, 7–13; females, which settle later: 1–4, 5, 6, 7–13) to account for the apparent increase in settlement rate with age (Piper et al. 2015). For Ψ_{TF} we added an early age interval, 1–6 years, to account for the apparent lower fighting ability of young males (Piper et al. 2015). Sparse data prevented a test of this age interval in females.

Comparisons between models that included or excluded specific age intervals allowed us to evaluate the impact of separately estimated age intervals on model fit. For example, we compared models for Φ_{terr} and Φ_{float} that presumed senescence in the 14–18 age interval to models that included no senescence (Table 1: model #1 vs. #2 and #5 vs. #6; Table 2: #1 vs. #5 and #6 vs. #9).

Three simple models served as a useful baseline for comparisons to others that were either more or less parameterized. The “constant” models held parameter estimates constant across all age intervals (#13 and #11 in Tables 1 and 2, respectively). The “full time” models presumed full time dependency across p , Φ , and Ψ (#12 and #13 in Tables 1 and 2). The “full age” models produced separate estimates for all age intervals of p , Φ , and Ψ (#9 and #12 in Tables 1 and 2).

Analysis of effect of age on body condition and behavior

As a possible measure of senescence, we compared change in body mass between males and females for those captured at least once between ages 5 to 12 and at least once at age 15 and older. In each case, we calculated change in mass as the mean for all captures from 5 to 12 subtracted from the mean for captures at age 15 or above. All masses were seasonally adjusted for date of capture.

We used generalized linear models to investigate the effect of age on chick feeding and chick attendance. Chick feeding rate was computed as the number of food items (fishes and invertebrates) fed by a parent to its chick or chicks per hour of observation. We then normalized the variable by taking its

natural logarithm and used it as the dependent variable and age as the sole independent variable in a generalized least squares regression (using the “xtreg” command in the STATA 14.2, College Station, TX, USA). Loon identity and territory were used as random effects because individual birds and territories contributed multiple observations to the analysis. Chick attendance was measured as the proportion of all five-minute scan samples in which a loon was within 20 m of one or both chicks and used as dependent variable in a GLS regression, again with age as the independent variable and identity and territory as random effects.

Territorial yodels typically occur not singly but in bouts consisting of two or more yodels, each bout representing a response to an intruder that has landed in the territory or if flying over it. We used number of yodel bouts by a given male in a given year as the dependent variable in a negative binomial regression analysis (“xtnbreg” in STATA), after validating that the data did not fit a Poisson regression model. Age was an independent variable, and number of intruders and flyovers during the year served as a covariate. As before, individual identity and territory were used as random effects to account for repeated measures.

Following validation, we used a Poisson regression analysis to analyze the number of aggressive events (battles, lunges, underwater attacks, or chases) in a given year by a given male or female, with age as an independent variable. Aggressive events are directed towards intruders; therefore, we included as covariate the total number of intruders into the territory in a given year. Again we included individual identity and territory as random effects.

Analysis of the effect of age on number and age of territorial intruders

Any apparent effect of a territory holder’s age on its territorial behavior might have been caused, instead, by the intruders that visited its territory. Thus, for breeders of both sexes, we examined the relationship between breeder age and the total number of intruders in a year. For male breeders only, we also examined the relationship between breeder age and (1) number of young (marked) male intruders and (2) mean age of male intruders (an indication of competitive ability, see Piper et al. 2015). Like aggressive events and yodels, numbers of intruders were analyzed as counts using negative binomial regression (following validation), with individual identity and territory as random effects. To control for differing duration of observations between breeder-years, duration of observation was added as a covariate. The relationship between male breeder age and male intruder age was analyzed with a mixed model that again had as random effects breeder identity and territory.

Table 1 Age intervals used in models tested for fit to male mark-resighting data in Program MARK. Each row lists the components of a unique set of separately estimated parameters according to age interval for survival of territory holders (ϕ_{terr}) and floaters (ϕ_{float}), resightings in each class (p_{terr} , p_{float}), and transitions from territory holder to floater or vice-versa (ψ_{TF} , ψ_{FT}). For example, model 1 estimated the survival of territory holders separately for two age intervals, 1–13 and 14–18, but used six separate parameters (for intervals 1–3, 4, 5, 6, 7–13, and 14–18) to estimate ψ_{FT} . Models are listed from best to poorest fit and include the “full age” model (model #9; every age interval estimated separately), the “full time” model (#12; each year estimated separately), and the “constant” model (#13; no age structure)

ϕ_{terr}	ϕ_{float}	p_{terr}	p_{float}	ψ_{TF}	ψ_{FT}	AICc	AICc wts	# param	Dev.
1 1–13, 14–18	<i>I</i> , 2, 3–13, 14–18	<i>I</i> –18	<i>I</i> , 2, 3, 4–18	1–6, 7–13, 14–18	1–3, 4, 5, 6, 7–13, 14–18	1828.77	0.6308	16	1134.63
2 1–18	<i>I</i> , 2, 3–18	<i>I</i> –18	<i>I</i> , 2, 3, 4–18	1–6, 7–13, 14–18	1–3, 4, 5, 6, 7–13, 14–18	1830.76	0.2337	14	1140.75
3 1–13, 14–18	<i>I</i> , 2, 3–13, 14–18	<i>I</i> –18	<i>I</i> , 2, 3, 4–18	1–6, 7–18	1–3, 4, 5, 6, 7–13, 14–18	1832.79	0.0843	15	1140.72
4 1–13, 14–18	<i>I</i> , 2, 3–13, 14–18	<i>I</i> –18	<i>I</i> , 2, 3, 4–18	1–6, 7–13, 14–18	1–3, 4, 5, 6, 7–18	1833.80	0.0511	15	1141.72
5 1–13, 14–18	<i>I</i> , 2, 3–13, 14–18	<i>I</i> –18	<i>I</i> , 2, 3, 4–18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1852.58	0	38	1111.65
6 1–18	<i>I</i> , 2, 3–18	<i>I</i> –18	<i>I</i> , 2, 3, 4–18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1853.56	0	36	1116.98
7 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	<i>I</i> , 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	<i>I</i> –18	<i>I</i> , 2, 3, 4–18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1885.13	0	63	1088.09
8 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	<i>I</i> , 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	<i>I</i> –18	<i>I</i> , 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1901.44	0	75	1076.27
9 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	<i>I</i> , 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	<i>I</i> , 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1937.86	0	94	1066.46
10 1–13, 14–18	<i>I</i> , 2, 3–13, 14–18	<i>I</i> –18	<i>I</i> , 2, 3, 4–18	1–6, 7–13, 14–18	1–13, 14–18	2033.09	0	12	1347.21
11 1–13, 14–18	<i>I</i> , 2, 3–13, 14–18	<i>I</i> –18	<i>I</i> , 2, 3, 4–18	1–18	1–18	2056.59	0	9	1376.85
12 All time intervals	All time intervals	All time intervals	All time intervals	All time intervals	All time intervals	2528.24	0	102	1636.74
13 1–18	1–18	1–18	1–18	1–18	1–18	2534.47	0	6	1860.84

Fixed parameters are shown in italic font. The last four columns list the AICc score, AIC weights, number of parameters, and deviance for each model

Table 2 Age intervals used in models tested for fit to female mark-resighting data in Program MARK. Each row lists the components of a single model consisting of a unique set of separately estimated parameters according to age interval for survival of territory holders (Φ_{terr}) and floaters (Φ_{float}); resightings in each class (p_{terr} , p_{float}); and transitions from territory holder to floater or vice-versa (Ψ_{TF} , Ψ_{FT}). For example, model 1 used only a single parameter to estimate the survival of

territory holders across all age intervals (1–18) but used four separate parameters for resighting of floaters (for intervals 1, 2, 3, and 4–18), etc. Models are listed from best to poorest fit and include the “full age” model (model #12; every age interval estimated separately), the “full time” model (#13; each year estimated separately) and the “constant” model (#11; no age structure)

	Φ_{terr}	Φ_{float}	p_{terr}	p_{float}	Ψ_{TF}	Ψ_{FT}	QAICc	QAICc wts	# param	Dev.
1	1–18	<i>1, 2, 3, 4–18</i>	<i>1–18</i>	1, 2, 3, 4–18	1–13, 14–18	1–4, 5, 6, 7–18	919.52	0.3773	13	567.51
2	1–18	<i>1, 2, 3, 4–18</i>	<i>1–18</i>	1, 2, 3, 4–18	1–18	1–4, 5, 6, 7–18	919.81	0.3267	12	569.91
3	1–18	<i>1, 2, 3, 4–18</i>	<i>1–18</i>	1, 2, 3, 4–18	1–13, 14–18	1–4, 5, 6, 7–13, 14–18	921.56	0.1361	14	567.42
4	1–18	<i>1, 2, 3, 4–18</i>	<i>1–18</i>	1, 2, 3, 4–18	1–18	1–4, 5, 6, 7–13, 14–18	921.88	0.1159	13	569.87
5	1–13, 14–18	<i>1, 2, 3, 4–13, 14–18</i>	<i>1–18</i>	1, 2, 3, 4–18	1–18	1–4, 5, 6, 7–18	923.82	0.0440	14	569.68
6	1–18	<i>1, 2, 3, 4–18</i>	<i>1–18</i>	1, 2, 3, 4–18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	965.42	0	39	555.04
7	1–18	<i>1, 2, 3, 4–18</i>	<i>1–18</i>	1, 2, 3, 4–18	1–13, 14–18	1–18	969.46	0	10	623.77
8	1–18	<i>1, 2, 3, 4–18</i>	<i>1–18</i>	1, 2, 3, 4–18	1–18	1–18	969.67	0	9	626.06
9	1–13, 14–18	<i>1, 2, 3–13, 14–18</i>	<i>1–18</i>	1, 2, 3, 4–18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	969.81	0	41	554.65
10	1–18	<i>1, 2, 3, 4–18</i>	<i>1–18</i>	1, 2, 3, 4–18	1–13, 14–18	1–13, 14–18	970.05	0	11	622.26
11	1–18	1–18	1–18	1–18	1–18	1–18	1067.25	0	6	729.84
12	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18	1073.10	0	92	519.20
13	All time intervals	All time intervals	All time intervals	All time intervals	All time intervals	All time intervals	1211.00	0	97	641.48

Fixed parameters are shown in italic font.

Inclusion of loons of estimated age

In order to increase statistical power, we included adults banded as adults (“ABAs”; $n = 171$ males; $n = 172$ females) as well as ABJs ($n = 81$ males; $n = 30$ females) in our analyses of the impact of age on parental care and territorial behavior, assigning male ABAs an age of five and female ABAs an age of seven at settlement (see Piper et al. 2015). Inevitably, this step added noise to the analysis, since some adults (170 of 454 adults in our analyses; 37%) were first marked as adults on territories not covered previously. However, most ages were accurate to within a few years, because (1) 81 of 102 masses (79%), 2186 of 2572 loon-years in the analysis of aggressive events (85%), 1244 of 1472 male-years from the yodel analysis (84%), and all feeding and attendance data were from 2000 or later, when all loons had been observed in the year of settlement, and (2) only one marked adult of 454 used in

our analyses has ever dispersed into our study area from an extensive study area that abuts ours to the north.

Data availability The datasets generated during and/or analyzed during the current study are available in the “Loon Project Database” repository through Chapman University Digital Commons, https://digitalcommons.chapman.edu/sees_data/3/.

Results

Resighting probability and survival

For both male and female analyses, two models that differed slightly in estimated parameters fell within 2 AICc (or QAICc) of each other (Tables 1 and 2), so we used model averaging to generate final estimates of parameters (Cooch and White

2006). Resightings of floaters, p_{float} (parameter estimate \pm SE), increased gradually during the 2nd (0.17 ± 0.03), 3rd (0.56 ± 0.05) and 4th to 18th age intervals (0.79 ± 0.03) in males and 1st (0.005 ± 0.006), 2nd (0.06 ± 0.02), 3rd (0.18 ± 0.04), and 4th to 18th age intervals (0.33 ± 0.04) in females.

Among males, apparent survival (Φ) of both territory holders and floaters was best estimated with two distinct parameters: a single one for age classes up to 13, which showed a high probability of survival and a second for ages 14 to 18 (Table 1: model #1 vs. #2, model #5 vs. #6), which showed a lower rate, especially among floaters (Fig. 1). In contrast, apparent survival among females was best estimated using a single parameter across all age classes for territory holders and across ages 4 to 18 in floaters (Table 2: model #2 vs. #5 and #6 vs. #9); thus, we found no evidence for an impact of age on survival in females (Fig. 1).

Loss of territory and body mass

The transition parameter, Ψ_{TF} , which signifies territory loss, revealed further evidence of senescence in males. The two best-fitting models contained the 14–18 age interval in Ψ_{TF} , which improved fit by 4 AIC_c (Table 1: model #1 vs. #3). Parameter estimates showed that rates of male territory loss were three times higher in the 14–18-year-old than in the 7–13-year-old age class (Fig. 2). Among females, inclusion of the 14–18 age interval for Ψ_{TF} improved fit by only 0.3 QAIC_c (Table 2: model #1 vs. #2) indicating ambiguity with respect to the added age interval. Parameter estimates, moreover, suggested that older females might be slightly less, not more, prone to territory loss (Fig. 2).

Males tended to lose body mass between ages 4 to 13 and age 14+ (mean change in seasonally adjusted mass \pm SE = $-56.0 \text{ g} \pm 24.9$, $n = 54$), while female mass showed little change ($+13.3 \text{ g} \pm 24.2$, $n = 54$; $t = 2.0$, $df = 106$, $p < 0.05$, two-tailed test between sexes).

Territory settlement and resettlement

Age structure in territory settlement and resettlement (Ψ_{FT}) was rather complex in both sexes. Among males, the model with six age intervals gained 204 AIC_c more support than one that lacked age intervals for young birds (Table 1: #1 vs. #10) and 5 AIC_c more support than the model lacking the 14–18 interval (Table 1: #1 vs. #4). Probability of settlement or resettlement increased steadily throughout the male lifespan (Fig. 3). The best female models for territory settlement included four estimated age intervals and, as in males, were far superior to comparable models lacking younger age intervals (by 50 QAIC_c; Table 2: #1 vs. #7, #2 vs. #8). On the other hand, models containing the 14–18 age interval showed poorer fit by about 2 QAIC_c (Table 2: #1 vs. #3, #2 vs. #4), indicating no impact of old age on resettlement. As in males, settlement rate generally increased with age, but females in the 7–13 and 14–18 intervals did not differ appreciably (Fig. 3).

The Ψ_{FT} transition comprised two distinct forms of settlement that varied with age. Ninety percent of 4- to 9-year-old males ($n = 124$) and all 4- to 9-year-old females ($n = 37$) that settled were prebreeders claiming a first territory. In contrast, 66% of males ($n = 41$) and 67% of females ($n = 49$) in the 10 to 13 year age class and 95% of males ($n = 22$) and 96% in females ($n = 23$) 15 and older were resettling after eviction.

Fig. 1 Estimates of annual survival (+ SE) for male ($n = 286$) and female loons ($n = 252$) from Program MARK



Fig. 2 Estimates of annual probability of territory loss (+ SE) for male ($n = 286$) and female loons ($n = 252$) from Program MARK



Young males had longer territory tenure and higher breeding success when resettling after eviction than did old males, partly owing to higher mortality in the latter group. Evicted males aged 5 to 13 years spent 3.7 years (± 0.37 SE, $n = 75$) on the new territory, while males 15 years and older spent only 2.3 years (± 0.54 SE, $n = 15$; $t = 2.2$, $p < 0.05$, $df = 57$; t test with unequal variances). In addition, males of 5 to 13 were more likely to produce chicks than 15+-year-old males (young 69%, $n = 73$; old 41%, $n = 17$; chi-squared = 5.0, $p = 0.03$). Among evicted females, 6 to 13 year olds settled on territories for a similar amount of time to 15+-year-old females (young 3.2 ± 0.37 years SE, $n = 43$; old 4.0 ± 0.61 , $n = 20$; $t = 1.3$, $p = 0.20$, $df = 69$) and did not differ from them in likelihood of

producing chicks (6–13: 47%, $n = 43$; 15+: 70%, $n = 20$; chi-squared = 3.0, $p = 0.08$).

Effect of age on chick feeding and attendance

There was no age-related pattern in the feeding or attendance of chicks in either sex based on analyses that all used bird and territory as random effects. That is, males did not increase their rate of chick feedings with age ($z = -0.11$, $p = 0.92$, $n = 91$; GLS regression). Females, likewise, showed no age-related increase in chick feeding ($z = 1.50$, $p = 0.13$, $n = 79$). Similarly, chick attendance did not vary with age in either

Fig. 3 Estimates of annual probability of territory resettlement (+ SE) for male ($n = 286$) and female loons ($n = 252$) from Program MARK



Table 3 Statistical results for negative binomial regression analysis that used yodel bouts per bird-year as dependent variable and both bird and territory as random effects. $N = 252$ individual males across 1472 bird-

Predictor variable	Coefficient	SE	z	p
Total number of intruders and flyovers	0.0553	0.00362	15.29	< 0.0005
Age	0.0430	0.0078	5.51	< 0.0005

males ($z = 0.98$, $p = 0.32$, $n = 91$ males) or females ($z = 0.41$, $p = 0.69$, $n = 78$ females).

Effect of age on territorial behavior, aggression, and intruders

Age affected male territorial behavior in two respects. Males in their late teens or twenties yodeled once, on average, for every three occasions when an intruder either flew over or landed on their lake. In contrast, younger males yodeled once roughly every four intruders (Table 3, Fig. 4). Second, likelihood of aggression directed towards a territorial intruder increased significantly with male age (Table 4), while aggression by female territory holders did not vary with age (Table 5).

Age of breeders had no apparent effect on either the number or age of intruders that landed in their territories. Neither total number of intruders ($z = 0.74$, $p = 0.46$, $n = 229$ males) nor number of known male intruders ($z = 0.97$, $p = 0.33$, $n = 237$ males) increased with age of male breeders. Similarly, female age had no detectable effect on total intruders ($z = -0.73$, $p = 0.46$, $n = 186$ females). Finally, intruders into territories

years. Yodel bouts by a given male in a given year is predicted by (1) the number of intruders + flyovers in that territory and year and (2) male age

defended by older male breeders were no older than intruders into young male breeders ($z = 1.00$, $p = 0.32$, $n = 156$ males).

Discussion

Once they reach their mid-teens, male loons senesce: they lose body mass, decline in survival rate (Fig. 1), and are often evicted from their territories (Fig. 2). At first glance, the high resettlement rate of 14–18-year-old male floaters (Fig. 3) would appear an exception to the low competitive ability of this age-sex class, but this pattern is deceptive. These males are evicted breeders with low fighting ability that typically settle on vacant territories without aggression (Piper et al. 2015). Vacant territories, moreover, often lack safe nesting habitat, a likely explanation for the poor breeding success of old males after resettlement. Hence, old male floaters are not successful competitors settling on established territories, but declining individuals that settle at a high rate on unproductive ones.

Senescence in survival, often termed actuarial senescence (Nussey et al. 2013), is widespread in vertebrates (Bouwhuys et al. 2012; Nussey et al. 2013). Nonetheless, senescence of

Fig. 4 Proportion of intrusions that elicited a territorial yodel (+ SE) by male age class. Sample sizes listed at top

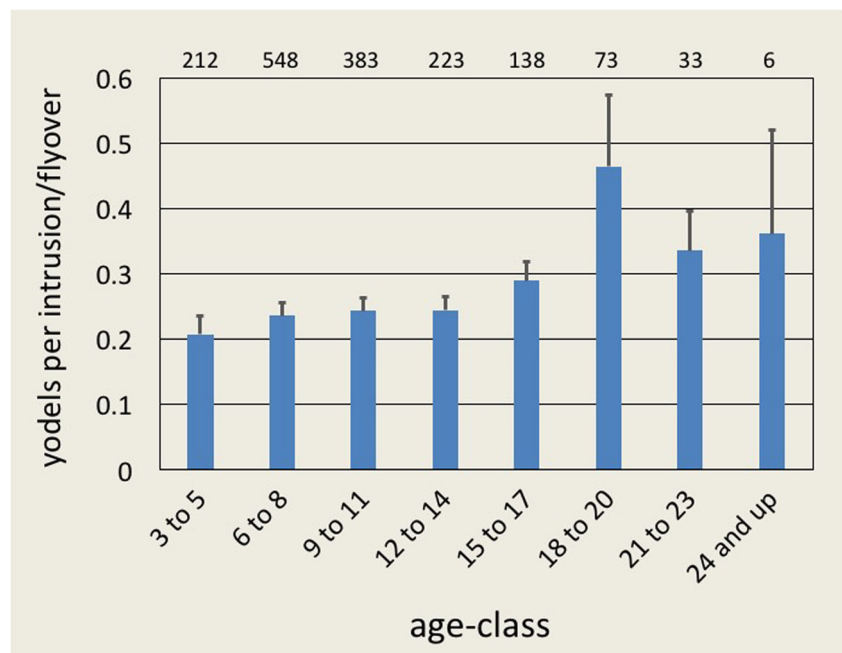


Table 4 Statistical results for Poisson regression analysis that used aggressive events per bird-year as dependent variable and both bird and territory as random effects. $N = 252$ individual males across 1374 bird-years. Aggression by a given male in a given year is predicted by (1) the number of intruders in that territory and year and (2) the age of the male

Predictor variable	Coefficient	SE	z	p
Total number of intruders	0.0565	0.00756	7.47	< 0.0005
Age	0.0398	0.0159	2.50	0.012

male loons in their mid-teens was unexpected, since our own recent investigation, conducted on successful breeders only, found that neither male nor female loons begin to senesce until their mid-20s (Piper et al. 2017). However, successful breeders, the class of individuals sampled most consistently by many field studies (e.g., Briggs et al. 2011; Fife et al. 2015), have competed for territories and produced young. Hence, this set of birds might not exhibit the patterns of aging found in the population at large. By sampling all loons of fledging age in the present study, whose ages were known precisely, we detected an “early tier” of senescence.

Male-biased senescence is rather common in vertebrates (Clutton-Brock and Isvaran 2007). Intense breeding competition, pronounced sexual dimorphism, and a large contribution to parental care are factors associated with high mortality within one sex (Promislow et al. 1992; Liker and Szekely 2005; Clutton-Brock and Isvaran 2007). Male loons are considerably larger than females, produce the male-only territorial yodel, and exhibit more aggression in territorial contests (Piper et al. 2008a). Yet males also contribute equally to incubation of eggs and provide more parental care to chicks than females do (Jukkala and Piper 2015). The combination of intense territorial aggression and substantial parental care makes male loons unusual among birds (Owens and Hartley 1998) and might explain the early wave of male senescence.

Early senescence depresses residual reproductive value in old males, setting the stage for terminal investment. Indeed, males 14 and older apparently make a terminal investment in breeding by resettling at a high rate after territorial eviction (Fig. 3), despite a low probability of breeding success.

Table 5 Statistical results for Poisson regression analysis that used aggressive events per bird-year as dependent variable and both bird and territory as random effects. $N = 206$ individual females across 1187 bird-years. Aggression by a given female in a given year is predicted by the number of intruders in that territory and year but not by the age of the female

Predictor variable	Coefficient	SE	z	p
Total number of intruders	0.0592	0.0108	5.50	< 0.0005
Age	0.0151	0.0232	0.65	0.515

Another likely terminal investment by old male loons is their stepped-up commitment to territory defense and aggression. Territorial yodels, more frequent in old than young males (Fig. 4), are employed during defense of territory and young (Mager et al. 2012; Jukkala and Piper 2015). Yodels are loud, complex calls that communicate identity (Walcott et al. 1999) and aggressive motivation to intruders (Mager et al. 2012). But yodels are also an honest signal of body mass and condition relative to past years (Mager et al. 2007). It seems that the benefits of conveying to intruders that they are likely to be attacked outweigh the drawbacks of informing them that their attacker is not in prime condition. The greater aggressiveness of older males implies that they are indeed willing to attack territorial intruders that ignore yodels and engage them. We presume that old hyper-aggressive males might, in some cases, be able to hold their territory for an extra year or two and produce a few more offspring.

As noted above, old males tend to reside on poor territories, so their increased aggression cannot be explained by higher territory quality. Since older males face neither more nor older male intruders than young males, increased territory defense and aggression of older male breeders did not seem to occur because they were intruded upon more often or by older, more aggressive intruders (Piper et al. 2015).

Existing reports of terminal investment in territorial aggression are scarce and problematic. The California gull (*Larus californicus*) exhibits apparent terminal investment, but the sharp increase in defense of nesting areas with age (Pugesek 1981) might simply show defense of chicks, not territory defense per se. Male banded wrens (*Thryophilus pleurostictus*) seem to increase territorial calling in their final year, but longitudinal analysis did not confirm this result (Hall et al. 2009). Similarly, male song sparrows (*Melospiza melodia*) show a possible increase in aggressive territorial defense with age, but a confound with past territory status renders the finding uncertain (Hyman et al. 2004).

Although we have shown that male loons begin to senesce rapidly in their mid-teens and also increase their territorial and aggressive behavior at this time, a more complete test of the terminal investment hypothesis requires a measurement of the fitness impact of this behavioral change (Clutton-Brock 1984). Despite the lengthiness of our study, we do not yet have sufficient data to establish this link.

Territorial behavior is metabolically taxing (Biro and Stamps 2010), and it is likely to exacerbate the physical decline of older males. More important, aggressive behavior towards a strong, motivated opponent is likely to escalate a territorial contest, increasing the likelihood that the aggressor will be seriously injured or killed (Waas 1991). In short, aggressive territorial defense by old male loons is a high-risk

strategy likely to culminate in the sort of fatal contests that occur commonly in males of this species (Piper et al. 2008a).

Acknowledgments We thank three collaborators, Charles Walcott, Jay Mager, and Joel Flory, and many research assistants, especially Andrew Reinke, Nathan Banfield, Keren Tischler, Margaret Klich, Frank Spilker, Lyla Furey, Erin Harrington, and Amy Turcotte. We also thank two anonymous reviewers.

Funding The research was supported by the National Science Foundation (IBN-0316442 and DEB-0717055), the National Geographic Society, the Disney Conservation Fund, and Chapman University.

Compliance with ethical standards

Ethical approval We followed all applicable international, national, and institutional guidelines for the care and use of animals. All protocols for capture, marking and study of common loons were approved by the Chapman University Animal Care and Use Committee.

Conflict of interest The authors declare that they have no conflict of interest.

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