Honest signalling of age in a territorial breeder

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Age often indicates phenotypic quality, ecological experience or social status in animals. Consequently, behavioural signals in territorial animals that accurately convey age to potential mates or rivals might provide useful information for both signaller and receiver about the likelihood of aggression. We tested whether male territorial yodels convey information about age in the common loon, *Gavia immer*. Using a sample of male loons of known age, we found that the dominant frequency of Fintro3, a dominant syllable in the beginning sequence of a male yodel, increases strongly with age, but we were unable to replicate an earlier finding linking Fintro3 to body mass. We hypothesize that older male loons, which yodel more often than young males, might do so as a means to advertise their age and higher likelihood of aggression to potential rivals.
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Many animals use behavioural displays to transmit information about territory boundaries, ownership or aggressive intent while minimizing direct physical conflict (Smith & Price, 1973). Acoustic calls are a common modality for such displays, as sounds can be efficiently transmitted over a wide spatial area and a calling individual may indicate its presence, aggressive intent, pairing status or condition via the acoustic parameters of the call (broadly reviewed in Marler & Slabbekoorn, 2004; Suthers et al., 2016). Territorial competitors also stand to benefit from heeding territorial calls as they can assess the condition and/or intent of the caller without risking an aggressive physical encounter (Smith & Harper, 1995).

Long-range signals are generally honest. That is, across a growing number of animals, including birds, mammals, anurans and insects, signals usually convey accurate information about the size, condition or status of the signaller (reviewed in Webster et al., 2018). In a typical honest-signalling system, individual variation of an acoustic attribute like pitch, duration or amplitude correlates strongly with size, condition or status of the signaller (Webster et al., 2018). However, dishonest signals can occur wherein an animal modifies a call to disguise or misrepresent its condition (Smith & Harper, 2003). In the context of territorial aggression, evolutionary theory suggests that a mix of honest and dishonest signals can maintain a stable signalling system (Adams & Mesterton-Gibbons, 1995), and applications of honest and deceptive communication have been documented across a wide variety of taxa (insects: Heinze & d'Ettorre, 2009; anurans: Bee, 2000; birds: Gil & Gahr, 2002).

Animals acquire skills as they age (Sharpe, 2005) and may also obtain information regarding opponents' fighting ability that improves their likelihood of winning conflicts (Fawcett & Johnstone, 2010). Information about fighting ability is especially valuable in species where an individual's fighting ability fluctuates over time. If age indicates fighting ability, then signallers might be expected to communicate their age to competitors to reduce costly interactions. Furthermore, competitors receiving signals that convey age should use this information to their advantage by avoiding contests with territory holders of high fighting ability and by challenging individuals of low fighting ability. Indeed, there are numerous examples where vocalizations convey the age of the caller in ways that are adaptive to signallers and receivers. In nightingales, *Luscinia megarhynchos*, older males may exhibit different song patterns compared to first-year males (Kiefer et al., 2011). Territorial black redstart, *Phoenicurus ochruros*, males responded more aggressively in playback experiments when presented with adult

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songs compared to subadult songs (Cucco & Malacarne, 1999). In primates, the vocalizations of older female Campbell's monkeys, *Cercopithecus campbelli*, elicited more call-back responses than did the vocalizations of younger females, although younger adults were significantly more vocal overall (Lemasson et al., 2010).

While considerable work has described how animal calls vary between discrete life stages (e.g. juvenile and adult; first-year versus second-year and older), most of this work has focused on short-lived animals or on a narrow span of life history. A distinct gap in our understanding at present concerns how vocalizations change over longer periods of the life history, including the entire lives of long-lived animals (Berg et al., 2020). Hence, we have little understanding of whether calls might indicate long-term condition or senescence of the signaller (Berg et al., 2020). Most animals experience a period of low competitive ability early in life, followed by a period of high competitive ability, then another period of low competitive ability as they senesce (Arcese, 1987; Clutton-Brock et al., 1979). Only detailed study of vocalizations throughout life can reveal the extent to which vocalizations signal age and/or competitive ability across the entire life span.

Common loons, *Gavia immer*, aquatic diving birds, provide an excellent study system in which to investigate acoustic signalling in a territorial species. Young adult floaters (nonbreeding individuals) of both sexes visit territories defended by established adults in order to learn about territory quality via social information (Piper et al., 2006, 2015). Following such prospecting, floaters often evict breeders and seize territories for themselves (Piper et al., 2000). Male loons on breeding territories produce a long-distance call, the yodel, during territorial interactions with floaters. The yodel is a complex multisyllabic call consisting of an introductory note that rises in pitch, followed by one or more frequency-modulated repeat syllables (Mager & Walcott, 2014). Yodels signal identity (Walcott et al., 1999) and aggressive intent (Mager et al., 2012) to floaters and also serve to discourage close approach when produced by males defending chicks (Jukkala & Piper, 2015). Moreover, older male loons (1) yodel more often than young males (Piper et al., 2018) and (2) show a higher level of aggression than young males (Piper et al., 2018). Hence, it is plausible that age might be encoded acoustically in the yodel as a means to convey the heightened degree of risk faced by territorial intruders, a strategy that would likely save energy both for receiver and signaller.

We recorded yodels within a study population of marked, known-age male loons whose territorial behaviour has been under investigation since 1993. Previous work within this population of loons showed that the frequency of the final note of the first syllable of a yodel (Fintro3; Fig. 1) covaries with mass (Mager et al., 2007). However, that study occurred before we had usable

information on age of yodelling males and examined only mass and body size as potential predictors of yodel frequency. Here, we re-examined potential predictors of yodel frequency, this time taking advantage of a large number of adult males banded as chicks that had settled on territories in the past 15 years and whose yodels we recorded. By using yodels recorded over 3 years, we were also able to assess whether interannual differences across years that would systematically affect all loons (i.e. food shortages or parasitic black flies) might influence condition (e.g. mass) and consequently yodel attributes. Hence, this new expanded analysis permitted us to explore the possibility that age might predict yodel frequency, in addition to or instead of body mass.

METHODS

Study Area

We investigated loon vocal behaviour from 2017 to 2021 within a 1700 km^2 study region in northern Wisconsin, U.S.A. that covers parts of Oneida, Lincoln and Vilas counties. The study area contains more than 200 glacial lakes surrounded by mixed hardwood and coniferous forest but is used extensively by humans for angling, boating and other forms of recreation. Loons breed in monogamous pairs on territories that comprise either entire small lakes (mean size ± SD: 55 ± 36 ha; 96 of 125 total pairs in 2017) or protected bays of large lakes (358 ± 347 ha; 29 pairs).

Capture and Marking of Loons

Beginning in 1991, we captured adult loons and their chicks by nocturnal spotlighting from a 4.3 m motorboat using a salmon landing net (Evers, 1993). Following capture, loons were (1) taken quickly to shore, (2) fitted with a single U.S. Geological Survey steel leg band and three plastic coloured leg bands in unique combination, (3) weighed with a hanging scale and (4) released with family members within their territory. Close to one-half of all young males marked as chicks return to the study area as adults (Piper et al., 2012) because of high juvenile survival and short-range dispersal (mean ± SD = 10.2 ± 7.0 km, $N = 131$); thus, male settlers of known age and natal origin accumulated in the study area whose yodels could be recorded.

Determination of Age and Mass

Yodelling males were of two kinds: 'adults banded as juveniles' were banded as chicks on their natal lakes and hence were of precisely known age and natal origin; 'adults banded as adults' were of unknown age. However, demographic study of territory settlement has shown that initial territory settlement of males usually occurs at roughly 5 years of age. Therefore, we assigned an age of 5 years to all male settlers in their first year on territory. Not all adult individuals are captured each year to collect morphometrics; therefore, we obtained an exact mass estimate if the male was captured during the same year that its yodel was recorded, or, if the male was not captured during the same year that its yodel was recorded, we used its most recent mass estimate from a previous year of capture. For each individual, we thus matched the acoustic properties of the Fintro3 syllable of its yodel with its exact or estimated age and with its exact or most recently measured mass. For individuals that we recorded over multiple years, we used in the analysis only the yodel from the earliest year. Sample sizes are shown in Table 1 for birds of known versus estimated age and for birds whose mass was measured during the same year versus the previous year(s) that their yodel was recorded.
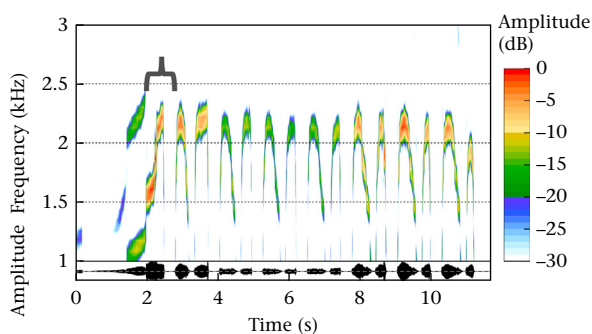

Figure 1. Spectrogram of an example yodel from male ArSMMb on Clear Lake, with Fintro3 (bracketed) and subsequent syllables highlighted.

Table 1
Sample sizes and year

Year	Age			Mass		
	Known	Estimated	Total	Known	Estimated	Total
2018	0	2	2	1	1	2
2019	9	14	23	5	18	23
2021	7	5	12	5	7	12
Total	**16**	**21**	**37**	**11**	**26**	**37**

Recording of Yodels

Observers in canoes approached male loons to within 20 m on the water and induced them to yodel using playback calls amplified with a digital speaker (AOMIS Sport II). From one to five yodels were collected from each male using digital recorders (Zoom H4n Pro Handy Recorders; Zoom North America, Hauppauge, NY, U.S.A.)

Acoustic Analysis

Acoustic recordings were digitized and analysed using the R packages warbleR, tuner and seewave and Raven Pro 1.5 software (Cornell University, Ithaca, NY, U.S.A.). In most cases (23 of 37 individuals), only a single yodel per individual was successfully recorded; therefore, we used only one yodel per individual in our statistical analyses rather than incorporate an 'individual' term in our models. For individuals with multiple yodel recordings within a year, we used only the first yodel recorded or the first clean yodel recorded without environmental noise or other acoustic degradation. For individuals recorded across multiple years, we used the most recent year recorded, e.g. the yodel representing the oldest age of the individual. Individual yodels were saved as .wav files and batch-visualized as spectrograms using the 'lspec' function in the warbleR package, retaining all vocalizations recorded between 0 and 6 kHz with a 10% overlap between consecutive windows. Spectrograms were visually assessed at this stage and discarded if the yodel spectrogram was not clear.

The autodetect function in warbleR was used to batch-detect shifts in vocalizations in all yodels, using an amplitude threshold of 15%, a minimum duration of 0.05 s and no maximum duration. These settings helped isolate the major codas of the yodel call and helped detect the start and stop times for Fintro3, the first ascending syllable of the loon yodel. When needed, the start and stop times for Fintro3 were also demarcated manually in the software Raven. We assessed signal-to-noise ratios across all complete spectrograms using the batch-processing 'signoise' function in warbleR, with a margin overlap of 0.04.

We used the function 'specan' in R to calculate acoustic parameters of interest in Fintro3, specifically the maximum dominant frequency (i.e. the highest dominant frequency reached by Fintro3), the minimum dominant frequency (i.e. the lowest dominant frequency shown in Fintro3 syllable) and the mean dominant frequency.

Statistical Approach

We used linear models and generalized linear mixed models to investigate the relationships between male age and the dominant frequency of the Fintro3 syllable and between male mass and dominant frequency. We modelled the effects of age and mass on Fintro3 together using a generalized mixed model, and separately using linear models in order to assess any potential interactions as well as their individual relationships. Because we had so few mass measurements from birds taken in the same year that their yodel

was recorded, we combined birds with 'same year' and 'previous year' mass measurements together within the same generalized mixed model and used the number of years (i.e. 'delay') since mass had been measured as a random variable to account for this variation in time. We then allowed the relationship of mass to vary with delay by both slope and intercept. We used this approach to try to accommodate the potential effects of age while acknowledging that not having same-year measurements was likely to add some error. To investigate the effects of age independently, we modelled birds of known age and birds of estimated age separately. For mass, we only modelled pooled values (i.e. both estimated and known mass measurements). We modified our P value using a sequential Bonferroni procedure to correct for multiple testing in interpreting all findings (Rice, 1989). Finally, to understand the overall relationship between age and Fintro3 while controlling for year and seasonality effects, both of which could influence condition in a standardized fashion, we employed a linear mixed model combining birds of known and estimated age and incorporated year and Julian date as random effects. All tests were run in R (R Core Team, 2021).

Ethical Note

All procedures with animals were performed in accordance with state and federal guidelines and were approved by the Chapman University Animal Care and Use Committee (number 2018- 435 03). Permits for capture and marking of loons were obtained from the U.S. Geological Survey (Permit number 22246) and the state of Wisconsin. Only noninvasive techniques were used and investigators never approached within 5 m of study animals during observations. Observers maintained a distance of at least 5 m from study animals when recording yodels. Mass measurements used in analyses were obtained from adult captures occurring as part of a long-term monitoring programme that has surveyed loons in the study region since 2000. We captured loons by spotlighting, placed them in vented bins for transport to shore, and then banded and weighed them as quickly as possible (always within 1 h). After banding, loons were released back into territories in family groups. We verified the continued health and safety of all banded loons with repeat visits to each lake following capture.

RESULTS

Yodels from 37 different males were used in our analysis. Of these, 16 were banded as chicks, so their exact age was known; 11 of these 16 were caught and weighed in the same year that their yodels were recorded (Table 1).

The generalized mixed model using 'delay' as a random variable for estimates of mass showed slight variation in intercepts, suggesting a marginal effect of mass, wherein heavier birds produced lower-frequency yodels (Appendix, Table A1, Figs. A1–A3). This effect was minimal compared to the dominant effect of age, however, and random effect plots further suggested that substantial variability in mass measurements was due to the error contained in estimating mass values. Age and mass effects were consequently examined separately in linear models.

The frequency of the introductory yodel note was significantly higher in old males than it was in young males. The effect occurred among males whose ages were known exactly and also when pooled together with loons of estimated age (Table 2, Fig. 2). Within known-age loons only, age explained 43% of the variance, whereas in all males, age explained 26% of the variance. In contrast, the dominant frequency of Fintro3 was not significantly associated with adult male mass ($P = 0.41$), where mass represented individual measurements from either the same year or a recent previous year that the yodel was recorded (Table 2, Fig. 3).

Table 2
GLM model terms for effects of age and mass on Fintro3 dominant frequency for all adult males

Model	Estimate	SE	t	P	F	R^2_{adj}
Pooled age (Intercept)	1.53	0.07	21.83	<0.001	13.9	0.26
Pooled age (Age)	0.02	0.0	3.72	<0.001		
Known age (Intercept)	1.34	0.11	12.26	<0.001	12.3	0.43
Known age (Age)	0.03	0.01	3.48	<0.004		
Pooled mass (Intercept)	2.18	0.47	4.65	0.00	0.41	0.01
Pooled mass (Mass)	0.00	0.00	−0.83	0.41		

Two models investigating the effect of age are presented, with a pooled model using birds of both known age and estimated age and a model using only adults of known age (i.e. adults banded as juveniles). A separate linear model is shown for the effect of mass on dominant frequency.

Year effects on birds that were recorded yodelling in multiple years showed that yodels recorded in 2021 had significantly decreased Fintro3 frequencies in younger birds, whereas older birds did not strongly vary by year (Appendix, Fig. A4).

DISCUSSION

Mager et al. (2007) reported that males with high body mass produced yodels of lower frequency in Fintro3 syllable. Our analysis, which unlike Mager et al.'s (2007), included age as a potential predictor as well as body mass, revealed that older males produced higher-frequency yodels and that body mass per se was not an important predictor. Since we recently learned that males undergo a pronounced senescence that includes loss of mass with age (Piper et al., 2018), it seems possible that Mager et al.'s (2007) apparent correlation between body mass and yodel frequency was instead driven by a hidden correlation between age and yodel frequency. That is, we suggest that Mager et al. (2007) found low-frequency yodels among heavier males because young males produce low-frequency yodels and are also heavy. Thus, one possibility is that mass and yodel frequency are well correlated within young adults but age exerts a more significant influence on yodel frequency as males age. While the mass measurements we used in this analysis were largely estimated from previous years and thus susceptible to error, the random effects associated with differently sized birds does suggest that mass might play a buffering role, wherein dominant frequency increases strongly with age, but heavier birds maintain the lowest-frequency yodels in their age cohort (Fig. 4 schematic, Appendix, Fig. A1). A second possibility is that mass
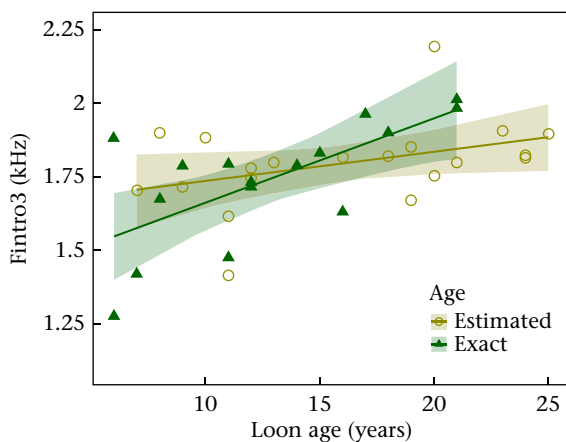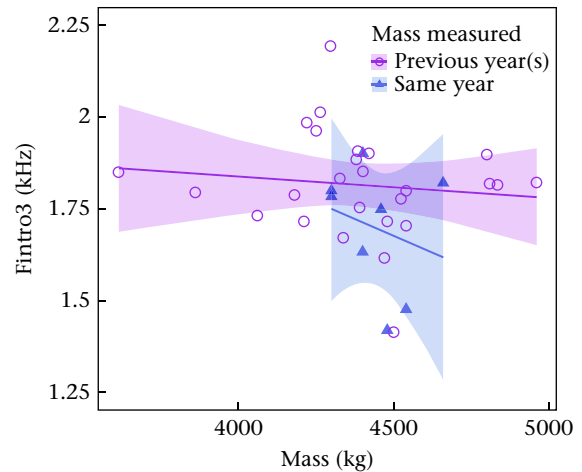

Figure 3. Relationship between the dominant mean frequency of the Fintro3 syllable and mass for adults weighed during the same year that their yodel was recorded and for adults whose mass measurements were used in the most recent previous year that they were caught.

and yodel frequency are not correlated and that Mager et al.'s (2007) apparent correlation reflects a type I statistical error. More concurrent observations of condition and yodels are needed to definitively understand the apparently contrasting roles of mass and age on Fintro3 dominant frequency.

It is unknown whether the increase in yodel frequency with age is under the male yodeller's control. If the acoustic parameters of the yodel are indeed plastic and subject to the caller's control, one might expect that a male's yodel would fluctuate substantially from one occasion to another, according to the context in which the call is given and the competitor to which it is directed. In fact, yodels produced by a single male are strikingly similar during a season and even between adjacent years, in most cases (Mager et al., 2010; Walcott et al., 1999), although changes in timing and frequency occur across years as do changes in territory status (Walcott et al., 2006). The general stability of yodels over time casts doubt on the yodel as a pliable signal that a male may adapt to suit his short-term needs.

Studies on changes in vocal attributes in older birds are uncommon, yet deterioration in vocal signals have been noted in wild great tits, *Parus major* (Rivera-Gutierrez et al., 2012), wild Seychelles warblers, *Acrocephalus sechellensis* (Berg et al., 2020) and captive swamp sparrows, *Melospiza georgiana* (Zipple et al., 2019). Moreover, the shift in vocal attributes between young and older captive birds in Zipple et al. (2019) was detectable by listening conspecifics during playback experiments and the calls of older birds evoked a significantly reduced aggressive response. The behavioural senescence hypothesis (Zipple et al., 2019) posits that ageing produces neural, hormonal or motor changes, and thus, senescence may result in an involuntary increase in the frequency of male loons' yodels.

If, as prescribed by the behavioural senescence hypothesis, the increase in frequency of yodels among older male loons results from inevitable physiological or neural changes that occur over time, then older males are, in effect, 'stuck' with high-pitched yodels that betray their age. While they may not be able to control this ontogenetic change in their territorial call, they can produce it more or less often. Since old male loons are notoriously aggressive and territorial (a 'terminal investment' that apparently evolved to help them retain their territories; Piper et al., 2018), we suggest that old males' tendency to yodel far more often than young males (Piper et al., 2018) might be an adaptive response to increased yodel

Figure 2. Relationship between the dominant mean frequency of the Fintro3 syllable and loon age for adults of known age (i.e. banded as first-year juveniles) and estimated age (i.e. individuals caught and banded as adults).
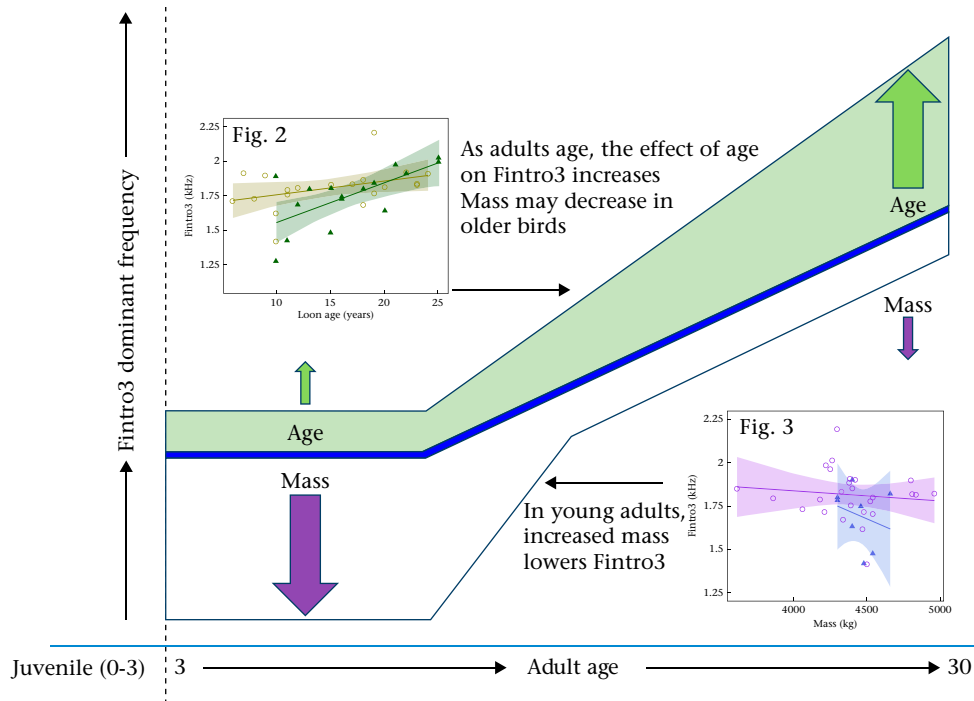
Figure 4. Schematic depicting one possible mechanism for the results linking mass and age with the Fintro3 dominant frequency. Age appears to exert a dominant effect by increasing the dominant frequency of the introductory phase of a yodel, yet this is mitigated by mass and condition so that larger individuals consistently give lower-frequency yodels. In the early phase of an adult's life, mass might play a larger role in shaping yodel dominant frequency, whereas in older birds, ageing might be the main driver of Fintro3 frequency.

frequency. That is, old males might yodel often in order to signal unambiguously to territorial competitors their willingness to use aggression to hold their territory as a means to reduce the rate of territorial challenges. The only recourse for an ageing male with a higher-frequency signature in his yodel may be to modulate his broadcast with a separate behavioural trait (yodelling frequency) that conveys increased aggression. In other words, old males might be taking advantage of an age-related increase in yodel frequency to send an adaptive signal to their territorial competitors.

Maturational changes in avian vocalizations are known in other birds (Berg et al., 2021; Kipper & Kiefer, 2010; Rivera-Gutierrez et al., 2012; Zipple et al., 2020) and mammals (Blumstein & Munos, 2005; Rogers, 2007; Root-Gutteridge et al., 2018). In birds, age-related changes have been primarily investigated in songbirds, in which substantial learning-based changes occur primarily between first-year birds and second-year birds in terms of song complexity, repertoire and length (e.g. Lapierre et al., 2011). Older classes of adult birds show high degrees of interspecific and intraspecific variation (reviewed in Kipper & Kiefer, 2010; see also Berg et al., 2021; Kochvar et al., 2022), making it difficult to discern trends. The relationship between signal variability and ageing among adults requires longitudinal data that necessitates following and recording individuals over time. This is a difficult endeavour outside of captive experiments and an especially difficult challenge when studying long-lived species.

Our results for common loons suggest that a strong relationship between ageing and signalling exists within a highly territorial species that competes vigorously for mates and territory. The behavioural implications of the pattern we describe, however, could be explored further. If age-related vocalizations in loons are used adaptively by males in territorial contests, measuring the responses of territorial loons to playback yodels of differing Fintro3 frequencies may help us understand whether age information is truly conveyed and acted on by other males. A playback

experiment by Mager et al. (2007) found that territorial males responded more quickly and with more yodels to low-frequency yodels played to them. While the experiment involved the rather rare scenario of an intruder yodelling at an owner, the fact that owners responded differently to high- and low-frequency yodels indicates that they can detect and respond to differences that convey age information. Hence, follow-up experiments that examine intruder responses to broadcast yodels of different frequency would provide further understanding of this rich behavioural system.

Author Contributions

W.H.P. conceived of the analyses and B.A.H. analysed the data. W.H.P. and B.A.H. both contributed to yodel data collection during the years of the study. B.A.H. wrote the manuscript with editorial suggestions from W.H.P., and both B.A.H. and W.H.P. participated in revising the manuscript.

Data Availability

Data from this paper are accessible in the 'Loon Project Database' at Chapman University Digital Commons (https://digitalcommons.chapman.edu/sees_data/3/), and the processed tabular data are provided as Supplementary Material. Acoustic files are too large to host, but processing script can be obtained via the corresponding author.

Declaration of Interest

We declare that we have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2024.01.004.

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Appendix

Table A1
GLMM results showing fixed and random effects for the model examining interaction effects of mass and age on dominant frequency, with a random term for 'weigh year' representing the number of years between a recorded yodel and the last time that individual was caught and weighed

Effect	Group	Term	Estimate	SE	Statistic
Fixed		(Intercept)	2.42	1.56	1.55
Fixed		Age	0.005	0.085	0.061
Fixed		Mass	−2.02e-04	0.00035	−0.575
Fixed		Age: Mass	−2.62e-06	1.89e-05	1.38
Random parameter	Weigh age	SD (Intercept)	0.964		
Random parameter	Weigh age	Cor (Intercept) mass	−1		
Random parameter	Weigh age	SD mass	2.83e-05		
Random parameter	Residual	SD observation	0.143		
Group	**Var1**	**Var2**	**V_cov**	**SD_cor**	
Weigh age (Intercept)			0.018	0.134	
Weigh age (Mass)			7e-10	2.68e-05	
Residual (0)			0.018	0.143	

Cor (Intercept) mass: estimated correlation between random intercept and slope of mass within weigh age levels; Var1: variance of first random effect; Var2: variance of 2nd random effect; V_cov: variance−covariance matrix of random main effects; SD_cor: standard deviations and correlations of random effects.

Table A2
GLMM model terms for the best-fit model using year as a nested random term to control for the influence of year of recording on the dominant frequency of the Fintro3 syllable in birds of known age ($N = 37$)

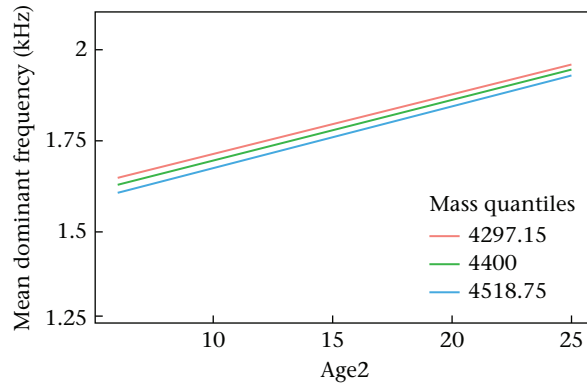| Model	Term	Estimate	SE/SD	t	Correlation of fixed effect
Fixed	(Intercept)	1.59	0.12	13.68	−0.953
	Age	0.02	0.01	2.19	
Random	Intercept	0.03	0.16		
	Year recorded	0.00007	0.01		

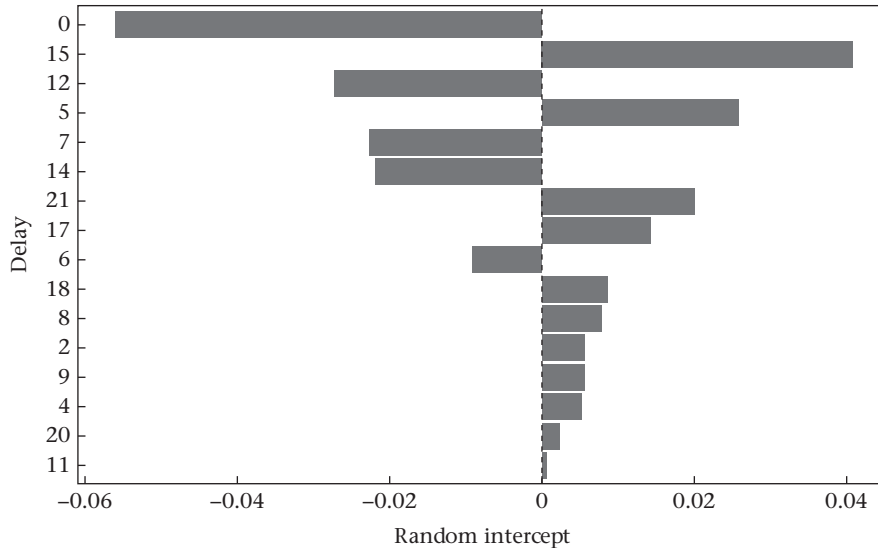**Figure A1.** Interaction of age and mass on mean dominant frequency.

Figure A2. Random effect bar plot depicting the random effect of years delayed (i.e. 'Delay') on the *y* intercept of mass. Estimates are ordered by decreasing magnitude.
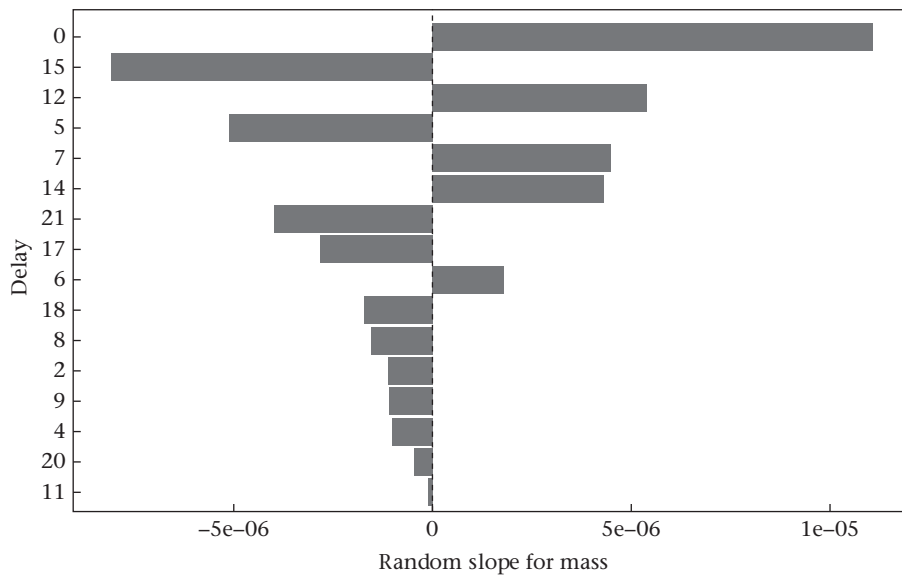

Figure A3. Random effect bar plot depicting the random slope effect of years delayed (i.e. 'Delay') on the relationship of mass and Fintro3. Estimates are ordered by decreasing magnitude.
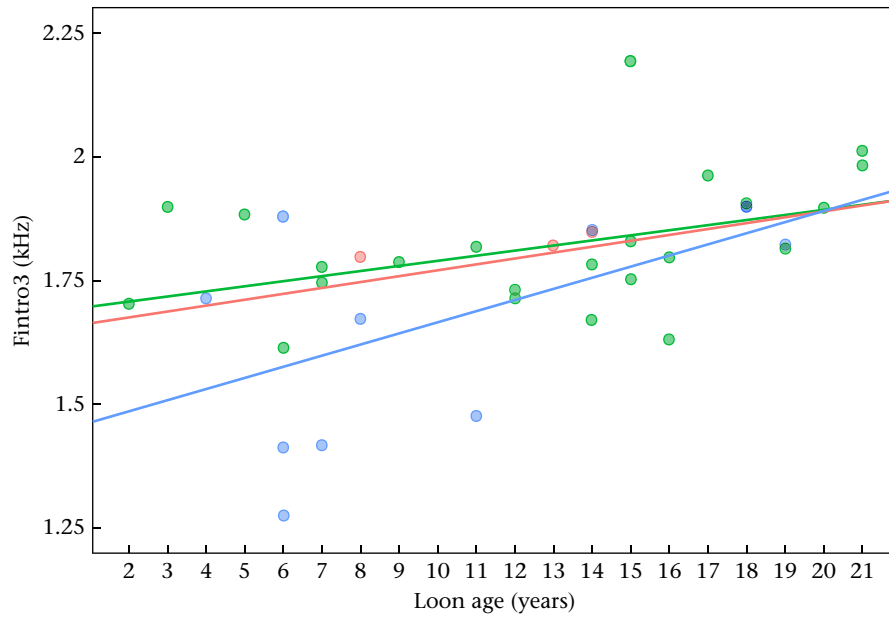
Figure A4. Relationship between the dominant mean frequency of the Fintro3 syllable and age in all loons (known and estimated) recorded during 2018 (red), 2019 (green) and 2021 (blue).