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ABSTRACT

Age is a critical metric for understanding the dynamics of wildlife populations. However, estimating the age of individuals in wild populations is challenging; while methods are available for aging dead animals (e.g., tooth sectioning), obtaining reasonably accurate age estimates of live, free-ranging animals is much more difficult. This is especially the case for cetaceans that move over large ranges, have an unpredictable occurrence, or may be cryptic in nature. We developed a protocol for deriving age estimates of false killer whales (*Pseudorca crassidens*) in Hawaiian waters using information curated from a long-term photo-identification catalog. The protocol integrates several qualitative lines of evidence (e.g., morphometric features, parentage, markings) into a quantitative framework for deriving age point estimates. Further, confidence ratings based on the strength and weaknesses of supporting evidence were developed to directly account for uncertainty in age estimates and scale the plausible range of ages (minimum and maximum) specific to each individual. While originally intended to inform a concurrent study on epigenetic aging of this population, our protocol provides a compelling alternative for estimating the age of individuals with common metrics from photo-identification catalogs and for which advanced genetic aging methods of biological samples (e.g., biopsies) are not feasible.

INTRODUCTION

Knowledge of the age of individuals is critical for understanding life history (e.g., age at first reproduction), social organization (e.g., age of dispersal), and for assessing population health (e.g., age structure to determine if populations are growing or shrinking), among other things. In limited cases, free-ranging individuals that have been live captured have had teeth extracted for aging (e.g., Hohn et al. 1989), and for some long-term studies where individuals are extensively photo-identified each year (e.g., Wells 2014), age of most individuals in the population may be known based on the year they are first seen. More recently, epigenetic aging methods have been developed for a few species either using samples available from dead individuals for which age can be independently determined (Bors et al. 2021) or based on populations with concurrent age information from photo-identification (e.g., Beal et al. 2019; Polanowski et al. 2014). However, for many populations and species of cetaceans, there are insufficient known-age individuals available to develop epigenetic models. As part of a collaborative effort to develop an epigenetic age estimation model for false killer whales in Hawaiian waters (Martien et al. in prep), we developed a method to estimate the age of individual false killer whales in Hawaiian waters using information available from a long-term photo-identification catalog (see Baird et al. 2008) in conjunction with sex information from biopsy samples (Martien et al. 2014), given sex differences in asymptotic length (Ferreira et al. 2014), as well as relative position of the dorsal fin on the back (Yahn et al. in revision) and a previously undescribed trait that appears to indicate physical maturity in male false killer whales. Although originally developed to inform the epigenetic aging work, this approach is of value for estimating age of false killer whales for a variety of other purposes, including informing the interpretation of results from aerial photogrammetry, assessment of age of animals acquiring evidence of fishery interactions, and association patterns based both on photo-identification and on simultaneous tag deployments. Here we outline the methods of this approach as they may be relevant for age estimation of other cetaceans for which similar lines of evidence are available.

METHODS

Each false killer whale that was biopsy sampled was photographed and compared to Cascadia Research Collective's (CRC's) long-term photo-identification catalog to determine individual identity (see Baird et al., 2008 for more details). The goal of the photo-ID based age estimation process was to estimate the age of individuals at the time of biopsy sampling for samples used in the epigenetic aging study, using all available evidence from the photo-identification work. The lines of evidence utilized include the years in which the individual was first seen and last seen, the year the individual was biopsied (when different from when first or last seen), the sex (from genetic analyses; see Martien et al. 2014), and several qualitative assessments such as the relative size of the individual to other individuals in photos (when available), the extent of markings on the dorsal fin when first seen (since markings accumulate with age), presence and degree of prominence of a leading edge hump at the base of the dorsal fin (indicative of physically mature males; Figure 1) and estimates of age class when biopsied (or tagged, as some individuals sampled for this study were also tagged at some point in their sighting history) by CRC.

A field assessment of combined age/sex class was often but not always made at the time of sampling or tagging by CRC based on size of the individual and the presence or absence of sexually-dimorphic characters: adult male, adult-female sized (which could be an adult female or a sub-adult male), sub-adult, juvenile, or calf. If an animal was considered "adult-sized" in the field but was not assigned a sex, we subsequently used genetic results and supporting qualitative data to consider it either an adult (if female) or sub-adult (if male). Field assessments were considered to be reliable estimates of age and sex, and were often used as reference points when assigning age/sex classes to other sightings within an individual's sighting history. The individual(s) responsible for the field assessments had substantial prior field experience with cetaceans in addition to false killer whales. Field assessment of age/sex class for samples collected by NOAA Fisheries were not used, although for the individuals sampled by NOAA Fisheries that were also sampled or tagged by CRC at some point during their sighting history the field assessments on those occasions were used.

If an individual was only seen once, the age classification relied heavily on the field assessment (see below). Cases where individuals were sampled subsequently to when they were first seen involved estimating age when first seen and adding the time period from this first estimate to when the animal was sampled for this study, provided this number didn't conflict with the field assessment (see below).

Age classification of individuals that were seen more than once was determined by first noting whether one or more field assessments for age and/or sex were recorded. For field assessments where both age and sex were recorded, the field classification of sex and the sex obtained from genetic analysis of the sample were compared; if the genetic results were the same as the field assessment, the age classification was considered highly reliable and was accepted unless there was a gross discrepancy when reviewing photos. However, if genetic results differed from the field assessment for sex, the age assessment was also questioned, as there is significant overlap in the sizes of adult females and sub-adult males. If a field assessment for age but not sex was recorded, the age assessment was reviewed using the sex (from genetic analyses) and the aforementioned series of qualitative assessments.

Reference ranges for age classes were generated separately for males and females: for females, a minimum age of 10 (i.e., the age at sexual maturity; see Ferreira et al. 2014) was assigned for adults, followed by 6-9 for sub-adults, and 3-6 for juveniles. For males, a minimum age of 15 was assigned for sexually-mature adults and 25 for physical-mature adults (the latter was determined either by the presence of a leading edge hump in photographs, through field assessment or for those in the catalog ≥25 years), with sub-adults ranging from 9-14 years, and juveniles 3-9 years. Although calves are seldom biopsied, calves for both sexes were assumed to be within 0-3 years of age.

For each individual in the epigenetic aging study, the age estimation process produced four values: a minimum and maximum age at the time of sampling (i.e., ages that we are 100% confident that the individual was no younger than or older than, respectively), a "best" age estimate, and a confidence rating on the best age estimate. Best age (in years) at the time of sampling was estimated by first considering the lower age point within the range for the individual's assigned age/sex class when the animal was first seen, and then adding the number of years between first seen and when it was sampled to derive a starting point for the best age estimate (see Eq. 1 in Appendix 1). Auxiliary data sources were incorporated into best age estimates when available (see Eq. 1), and include evidence from photographs (e.g., relative size, markings, dorsal fin shape), genetic parentage (e.g., offspring or parent of another individual, see Martien et al. 2019), and age estimates from tooth sectioning on stranded whales. Detailed examples on how these types of information were involved in age point calculations are provided in Appendix 1. For example, if a whale was first seen as an adult female in 2000 (sexually mature female age = 10 years) and biopsied in 2015, we would estimate a best age of 25 years old in the absence of other informative data sources. A confidence rating (1 = low, 5 = high) was determined for each best age estimate based on the quantity and quality of information supporting the estimate; general examples of criteria for assigning confidence ratings are listed at the end of the document. Primary factors affecting uncertainty in age estimates involve the span of years the individual was seen prior to being sampled, the age class when the individual was first sighted, and whether more definitive lines of evidence, such as genetic parentage, were available to inform the estimate. For example, if an animal assessed in the field as an adult male or adult female was biopsied during the same encounter when it was first sighted and no other information was available to guide a plausible age range (i.e., older or younger adult), then we chose 30 years as the best age, with a confidence rating of 1. In contrast, some individuals sampled were first documented when young (i.e., a juvenile or sub-adult), and as such, the range of plausible ages is narrower and we can be more precise in deriving a best age estimate (confidence = 4 or 5). In several cases, it was known that an individual was sexually mature, either based on known parent-offspring relationships (from Martien et al. 2019) or presumed in the case of sexually mature females from photographs documenting small calves in close association. In these cases, this information was used to back-calculate a plausible age based on age at sexual maturity and relative age of the offspring.

Minimum age was estimated by starting with the typical age for one age/sex class lower than the age classified when first seen, and adding the number of years prior to being biopsied to derive an overall minimum age estimate at the time of sampling (see Eq. 2 in Appendix 1). For example, if a biopsied whale was classified as an adult female at the time of biopsy but was first seen five years earlier, we would assume it could be no younger than six years old (sub-adult range 6-10 years) when first seen and thus a minimum of 11 years when biopsied. For younger individuals, a lower minimum age was set either based on the number of years seen or set at two years, since no calves thought to be younger than two (based on size) have been biopsied.

Maximum age estimates were determined through a set of rules that consider the age/sex classification of the individual at the time of sampling and the confidence rating associated with the individual's best age estimate at the time of sampling (see equations and examples at end of document). With this approach, the range of plausible maximum age estimates is scaled by the quantity and quality of supporting information available on each individual, such that individuals with strong supporting information have maximum estimates closer to their best age and those with poor supporting information have maximum estimates farther from their best age. An additional criterion was considered for adult maximum age estimates that accounts for the last year the animal was seen after sampling. Here, we assume that adult whales can be no older than 65[1] at any point during their sighting history; as such, if an adult was seen several years after sampling, then the maximum age at sampling would be less than 65 (specifically, 65 minus the years between last seen and sampling, Eq. 4). Therefore, a maximum age estimate based on confidence rating and a maximum age estimate based on the last year seen (assuming maximum possible age of 65 years at last year seen) were calculated for adults, and the estimate that was lower was assigned as the overall maximum age estimate for adults. With this approach, we accommodate for situations that may include individuals with strong supporting evidence leading up to sampling (i.e., maximum age estimate closer to best age estimate), and also for those with more limited histories prior to sampling but that have post-sampling sightings that provide enough foresight to warrant a lower maximum age estimate.

Rules for determining maximum age estimates based on confidence ratings are as follows: For adults (both sexes) with confidence ratings of 1 or 2 (poor support), the maximum age estimate at the time of biopsy sampling was set to 65[1]. Maximum age estimates for adults with best age confidence ratings of 3 (intermediate support), 4 (moderate support), and 5 (high support) were calculated as the best age point estimate plus 20 years, 15 years, and 10 years, respectively. The rules for sub-adults and juveniles followed a similar approach, albeit with a shorter scale and smaller range of years added to best age estimates, as the range of plausible ages for younger individuals is much narrower than that for adults. Maximum age estimates for sub-adults (both sexes) were calculated as follows: for confidence ratings of 1 or 2, maximum age was the best age point estimate plus 10 years; if the confidence rating was 3, maximum age was the best age point estimate plus 5 years; lastly, if the confidence rating was 4 or 5, the maximum age was the best age point estimate plus 3 years. The maximum age estimate rules for juveniles (both sexes) were on the same scale of confidence rating intervals as sub-adults, with the number of years

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[1] Sixty-five was chosen as the maximum age attainable, based on Ferreira et al. (2014), with a sample size of 65 aged males and 121 aged females.

added to the best age point estimate set to 5 years, 3 years, and 2 years for confidence ratings of 1-2, 3, and 4-5, respectively.

CONCLUSIONS

The methodology presented here provides a comprehensive and straightforward approach towards estimating the age of photo-identified individuals. Importantly, our methodology is structured to incorporate a variety of age-related information while also accounting for uncertainty associated with the lines of supporting evidence (or lack thereof) used to derive age point estimates. The amount of information available on a given individual can be highly variable across the sample population, even for extensive photo-identification catalogs curated over several decades. Our methodology allows for such case-by-case variability (e.g., confidence ratings and scaled age estimates) while also maintaining a consistent and pragmatic approach that can be applied to an entire sample population. Although a number of types of supporting information were used to derive age estimate equations here (Appendix 1), this general protocol could be easily modified to involve metrics that may be more specific to a particular population or photo-identification catalog with more or less available information.

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Figure 1. An adult male false killer whale showing the hump at the leading-edge base of the dorsal fin indicative of older males. This individual (HIPc205) was considered a juvenile when first documented in February 2001, assessed in the field as adult female-sized when biopsied in 2010, and last seen in September 2021. Using the protocol outlined in Appendix I, we estimated this individual to be 12 years old (range: 10-15 years old) at the time of sampling (2010) with good confidence (CR = 4) based on the young age class when first documented, span of years since first seen (10 years), and agreement between field assessment and derived age estimate (adult female-sized/sub-adult male). Therefore, this individual was likely around 23 years old when this photo was taken in September 2021, which is the approximate age we would expect to see the leading-edge hump shown in this photograph. © Doug Perrine, used with permission.

Appendix 1

Catalog-based age estimate equations and descriptions

Age point estimate equations:

(1) Best age: $Age_{best} = Age_{C,s1} + (Year_b - Year_{s1}) \pm Aux$

(2) Minimum age: $Age_{min} = Age_{C-1,s1} + (Year_b - Year_{s1}) \pm Aux$

(3) Maximum age, non-adults: $Age_{max} = Age_{C_{maxCR}}$

(4) Maximum age, adults:

If: $Age_{C_{maxCR}} < (65 - (Year_{ls} - Year_b))$

Then: $Age_{max} = Age_{C_{maxCR}}$

Else: $Age_{max} = (65 - (Year_{ls} - Year_b))$

Variable descriptions:

- $Age_{C,s1}$ = lower age point within the range for the individual's age/sex classification (C; adult, sub-adult, or juvenile) when first seen (s1 = sighting 1); see age values for C below. Therefore, (C-1) indicates one age classification lower (i.e., if C = adult, then C-1 = sub-adult)

- $(Year_b - Year_{s1})$ = number of years between biopsied year (b) and year first seen (s1)

- Aux = increase or decrease in age point estimate in consideration of auxiliary information (see details on auxiliary information below)

- $Age_{C_{maxCR}}$ = maximum age estimate for the individual based on age/sex classification and scaled by confidence rating, CR (i.e., how much information we have to be confident in the best age estimate).

- $(Year_{ls} - Year_b)$ = number of years between year last seen (ls) and year biopsied (b)

Values for age/sex classifications (Age_C):

- Adult female = 10 years (i.e., age at sexual maturity)
- Adult male, physically mature (from field assessment (FA) or photos) = 25
- Adult male, sexually mature/younger adult (from FA or photos) = 15
- Sub-adult female = 6
- Sub-adult male = 9
- Juvenile (male and female) = 3
- Calf (male and female) = 0-3 (information from sightings and photographs (e.g., relative size) inform age point within 0-3)

General examples of criteria for assigning confidence rating (CR):

- $CR = 1$: First seen when biopsied and FA was adult, no other auxiliary information
- $CR = 2$: Limited sighting history, but one level of auxiliary information available (e.g., physically mature male)
- $CR = 3$: Sighting history and/or auxiliary information provide reasonable evidence for age, although precision may be low (e.g., if seen several years later as adult, range of possible age at sampling narrower)
- $CR = 4$: Sighting history and auxiliary information provide strong evidence for age (e.g., long-term sighting history/span of years seen and/or genetic parentage information); younger individual so range of plausible ages is narrower
- $CR = 5$: Extensive sighting history and/or genetic parentage; age from tooth sectioning (stranded animals only); younger individual so range of plausible ages is narrower (especially when sighted several times)

Rules for maximum age estimates based on best age estimate confidence rating at time of sampling ($Age_{C_{maxCR}}$)

- Adults:
  - If $CR \leq 2$, then $Age_{C_{maxCR}} = 65$
  - If $CR = 3$, then $Age_{C_{maxCR}} = Age_{best} + 20\ years$
  - If $CR = 4$, then $Age_{C_{maxCR}} = Age_{best} + 15\ years$
  - If $CR = 5$, then $Age_{C_{maxCR}} = Age_{best} + 10\ years$
- Sub-adults:
  - If $CR \leq 2$, then $Age_{C_{maxCR}} = Age_{best} + 10\ years$
  - If $CR = 3$, then $Age_{C_{maxCR}} = Age_{best} + 5\ years$
  - If $CR \geq 4$, then $Age_{C_{maxCR}} = Age_{best} + 3\ years$
- Juveniles and calves:
  - If $CR \leq 2$, then $Age_{C_{maxCR}} = Age_{best} + 5\ years$
  - If $CR = 3$, then $Age_{C_{maxCR}} = Age_{best} + 3\ years$
  - If $CR \geq 4$, then $Age_{C_{maxCR}} = Age_{best} + 2\ years$

Types of auxiliary information incorporated into age point estimates (*Aux*):

- ***Photographic evidence:*** Often this line of evidence provided sufficient information to make distinctions within age classes
  - The presence of a leading-edge hump in the dorsal fin in males provides evidence for physical maturity (25 years)
  - Parentage assumed from repeated presence of calf. Example:
    - Repeated association of calf with adult female over time compelling enough to assume adult female is likely the mother, although cannot confirm due to lack of sample from presumed offspring. Therefore, add

        years to age estimates based on estimated age of offspring following the same approach detailed under “Genetic Parentage” below.
        - Note: ambiguous parent-offspring relationships inferred from photographs were not incorporated into age estimate calculations.
    - Relative body size, markings, and dorsal fin shape can indicate the individual is a young or old adult and similarly young or old sub-adult. Example:
        - Male first seen in 2006 and classified as a juvenile based on markings and relative size; biopsied in 2010 and classified as sub-adult (no sex) in the field.Considering this information and using the equations above, we derive:
            - $Age_{best} = 3 + (2010 - 2006) + Aux(X, FA) - Aux(X, photos) = 7$
            - $CR = 5$; first documented when young, span of years seen relative toyoung age classification
            - $Age_{min} = 1 + (2010 - 2006) + Aux(X, FA) - Aux(X, photos) = 5$
            - $Age_{max} = 7 + 5 = 12$

        In the above example, the photographic evidence indicated that the whale was likely a young juvenile when first seen, and then was classified as a sub-adult in the field when biopsied four years later (no sex). Because this whalewas genetically identified as a male, the best age estimate would suggest it was an older juvenile at the time of sampling (sub-adult male $Age_C = 9$),but could have been the relative size of a sub-adult female ($Age_C = 6$) when assessed in the field during sampling. As a result, the two available *Aux* terms essentially cancel out in this individual’s age equations.

- ***Genetic parentage:*** Many biopsies in this study have been analyzed for genetic parent/offspring relationships. We can use this type of information, combined with year first seen and age classifications when seen, to derive plausible age estimates for parents and/or offspring (i.e., parent must have been at least the age at sexual maturity (10 for females, 15 for males) at the estimated birth year of offspring). Consider the following hypothetical example:
    - Adult female X is the mother. First seen in 2000 and classified as adult based on relative size, markings from photographs; biopsied in 2005 with adult (no sex) field assessment.

    - Adult male Y is the offspring. First seen in 2002 and classified as an adult male from presence of leading-edge hump in dorsal fin. Biopsied in 2005, again classified as an adult male based on the field assessment.

    - First estimate offspring's best age, represented by Age_{Best_O}.
        - The age classification indicates that this adult male was physically mature when first seen and confirmed when biopsied a few years later ($Age_{C,s1} = 25$).
        - Using the equation for best estimate, we get:
            - $Age_{Best_O} = 25 + (2005 - 2002) = 28$ years old in 2005

  - Now estimate the mother's age incorporating this auxiliary information, represented by Age_{Best_M}
    - If offspring Y was 28 years old in 2005, then they would have been 23 in 2000 when mother X was first seen (born around 1977). Mother X would have to be at least 10 years older (i.e., age at sexual maturity) than offspring Y.
    - Using the equation for best estimate and adding the estimated age of offspring Y when mother X was first seen derives
      - $Age_{Best_M} = 10 + (2005 - 2000) + Aux(23, parentage) = 38$ years old in 2005.

  - Now estimate the confidence rating for both individuals' "best" estimates, as well as the minimum and maximum age estimates following the equations at the top of the document
    - Confidence rating for both mother X and offspring Y = 3; sighting histories are limited, but photographic evidence, field assessments, and genetic parentage support mid- to older age estimates.
    - Mother X minimum, using sub-adult female age (C-1):
      - $Age_{min_M} = 6 + (2005 - 2000) + Aux(23, parentage) = 34$
    - Offspring Y minimum, using sexually mature/younger adult level for males (C-1):
      - $Age_{min_O} = 15 + (2005 - 2002) = 18$
    - Mother X maximum, using CR = 3:
      - $Age_{max_M} = 38 + 20 = 58$
    - Offspring Y maximum, using CR = 3:
      - $Age_{max_O} = 28 + 20 = 48$

- ***Age from tooth sectioning:*** This type of information is only available for a few individuals included in this study that stranded and had age estimated from tooth sectioning analysis. Because this type of information has more precision and strength than photo-identification methods, age estimates for this study were estimated using the age at stranding (from tooth sectioning) as an anchor (i.e., back-calculating from stranding to biopsy when applicable).

- ***Age point estimates for individuals with limited supporting information:*** If all of the following criteria are met,
  - $(Year_b - Year_{s1}) = 0$ (i.e., animal first seen when biopsied)
  - $Aux = NA$ (i.e., no other information available on animal
  - $CR = 1$ (low confidence in best age estimate)
  - Assessed as adult male or female in the field

  Then the age estimates are assigned as follows:
  - $Age_{best} = 30$
  - $Age_{min} = 10$
  - $Age_{max} = 65$