

1 **Vibrissae length as a morphological proxy for**
2 **foraging behaviour in pinnipeds**

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15 ABSTRACT

16 Foraging behavior is a key driver of ecological and evolutionary processes, with individual
17 specialization shaping how populations respond to environmental change. Polymorphisms in foraging
18 strategies can both enhance and limit behavioral flexibility at the population level, making it crucial to
19 study individual variation. However, studying foraging is notoriously difficult, and while biologging
20 has significantly advanced our understanding of individual specializations, its limitations in sample size
21 and potential ethical concerns highlight the need for alternatives. In this study, we introduce a
22 complementary, non-invasive method using relative vibrissae length (RVL) measured from images as a
23 morphological proxy for foraging strategy in Galápagos sea lions (*Zalophus wollebaeki*). RVL differs
24 significantly between distinct foraging behaviours: benthic foragers have shorter vibrissae due to
25 abrasion, compared with pelagic foragers. Our method proved highly reliable, demonstrating strong
26 intra- and inter-observer repeatability as well as within-season consistency. Moreover, RVL remained
27 stable across multiple years, indicating long-term persistence in individual foraging specialization.
28 Vibrissae length thus exemplifies how behavioral specializations can shape morphological traits within
29 an individual's lifetime, offering a novel approach to study ecological polymorphisms. The integration
30 of RVL assessments with existing tracking methods can enhance sample sizes and improve our
31 understanding of individual foraging specialization at the population level. Our approach bridges the
32 gap between high-resolution data and broader-scale ecological monitoring, providing a scalable tool for
33 studying foraging strategies in pinnipeds.

34 INTRODUCTION

35 Foraging behaviour plays a fundamental role in shaping the ecology of species, populations, and
36 individuals. Since foraging directly influences energy acquisition, it affects key life-history traits such
37 as survival and reproduction (Davies et al., 2012). Therefore, understanding how diverse foraging
38 behaviours arise and their consequences on population dynamics is essential for comprehending broader
39 ecological patterns (Bolnick et al., 2003). While species or populations may appear to be generalists,
40 they often consist of ecologically diverse individuals that differ in foraging behaviour and resource use
41 (Araújo et al., 2011; Bell et al., 2009; Bolnick et al., 2002). This variation can have significant
42 implications for how populations adapt to environmental change (Arroyo et al., 2017) and cope with
43 ecological pressures.

44 Recent studies provide growing evidence of widespread behavioural variation and polymorphism within
45 populations (Araújo et al., 2011; Robertson et al., 2014; Toscano et al., 2016). While foraging behaviour
46 is often examined at the species or population level, individual specialization, where individuals
47 repeatedly use a limited subset of available resources, has emerged as a key factor in ecological research
48 (Araújo et al., 2011; Bolnick et al., 2003). Foraging strategies can differ significantly among individuals
49 of the same population, age, and sex, making it crucial to study these variations to gain a more
50 comprehensive understanding of foraging ecology (Bolnick et al., 2003). These differences can
51 influence competition, resource partitioning, and ultimately, a population's structure and ability to cope
52 with shifts in the environment (Araújo et al., 2011; Bolnick et al., 2003; Sargeant, 2007). Understanding
53 individual foraging behaviour is therefore not only a step toward refining ecological models but also a
54 crucial component in predicting species responses to environmental change.

55 Measuring individual foraging differences in the wild is challenging, particularly when large sample
56 sizes are needed to assess the ecological and fitness consequences. Biologging has transformed this field
57 by enabling detailed behavioural tracking, especially in cryptic or hard-to-observe species like marine
58 animals. These devices provide crucial insights into movement, diving behaviour, and resource use,
59 uncovering specialized foraging strategies across diverse taxa (Block et al., 2011; Watanabe &
60 Papastamatiou, 2025), including pinnipeds (Baylis et al., 2015; Breed et al., 2011; Jeanniard-du-Dot &

61 Guinet, 2021). However, despite its advantages, biologging has limitations. Attaching devices is often
62 invasive, raising ethical concerns and potentially affecting behaviour (Horning et al., 2019).
63 Additionally, logistical and financial constraints restrict sample sizes, making it difficult to study long-
64 term adaptation and fitness consequences. While biologging technology is advancing with devices
65 becoming smaller, more powerful and efficient (Wilmers et al., 2015), complementary, non-invasive
66 methods could expand sample sizes and enhance long-term monitoring of individual foraging strategies.

67 Morphological traits can serve as valuable proxies for foraging behaviour, offering a non-invasive way
68 to infer how individuals interact with their environment, especially when being able to be measured
69 from a distance. External features have long provided indirect but reliable insights into animals feeding
70 behaviour. Classic examples include the specialized beak shapes of Crossbills (*Loxia curvirostra*,
71 Benkman, 1993) and the body and wing shapes in bats reflecting their foraging styles (Fenton &
72 Bogdanowicz, 2002). Typically, these relationships between external morphology and foraging
73 behaviour emerge at the species level through long-term evolutionary processes. However, differences
74 that develop within populations and an individual's lifetime have been documented. In Eurasian
75 oystercatchers, individual feeding specialization in prey type and handling leads to morphological
76 differentiation in bill shape (Swennen et al., 1983; Van De Poll et al., 2009). By identifying such
77 measurable traits linked to foraging specialization, researchers can assess behavioural patterns across
78 larger sample sizes than biologging typically allows.

79 One such proxy has been identified in Galápagos sea lions (GSL), a species known to exhibit foraging
80 polymorphism (Jeglinski et al., 2013; Schwarz et al., 2021; Villegas-Amtmann et al., 2013). The isolated
81 and fluctuating environment of the Galápagos Archipelago challenges resident species to adapt to
82 variable conditions (Grant & Grant, 2014; Wikelski & Thom, 2000), making it an ideal place to study
83 behavioural flexibility and specialization. Schwarz et al. (2022) could identify that specialized foraging
84 behaviours result in distinct and temporally stable patterns of vibrissae abrasion, making it possible to
85 use vibrissae length retrieved from photographs as an indicator for foraging. Individuals foraging
86 benthically along the seafloor and hunting for prey on and in the sediment showed stronger abrasion and
87 consequently shorter vibrissae compared with pelagic foragers hunting in the open water column. This

88 highlights how even in species with diverse prey availability, such as GSL, individuals may exhibit
89 feeding specializations with limited behavioural plasticity (Schwarz et al., 2022; Swennen et al., 1983)
90 and studying morphology could provide valuable insight.

91 The aim of this paper is to provide a detailed evaluation of using relative vibrissae length (RVL) from
92 images as a proxy for foraging behaviour and assess its applicability. Specifically, we test both intra-
93 and inter-observer repeatability as well as repeatability across photographs to demonstrate the reliability
94 of this methodological approach. By analysing RVL also across multiple years, we demonstrate the
95 temporal stability of foraging strategy over time. Further, we explore whether differences in RVL are
96 exclusive to adults or already detectable in juveniles. Beyond establishing RVL as a behavioural marker,
97 we discuss the broader implications of using vibrissae length as a non-invasive alternative to biologging,
98 highlighting both its advantages and limitations. Our approach not only offers a potential tool for
99 studying other pinniped species, but also highlights the potential external morphology has in
100 representing behavioural polymorphism for ecological research. Ultimately, our findings illustrate how
101 a non-genetic variation in morphological traits can provide unexpected insights into an animal's foraging
102 strategies.

103 MATERIALS AND METHODS

104 **Study details**

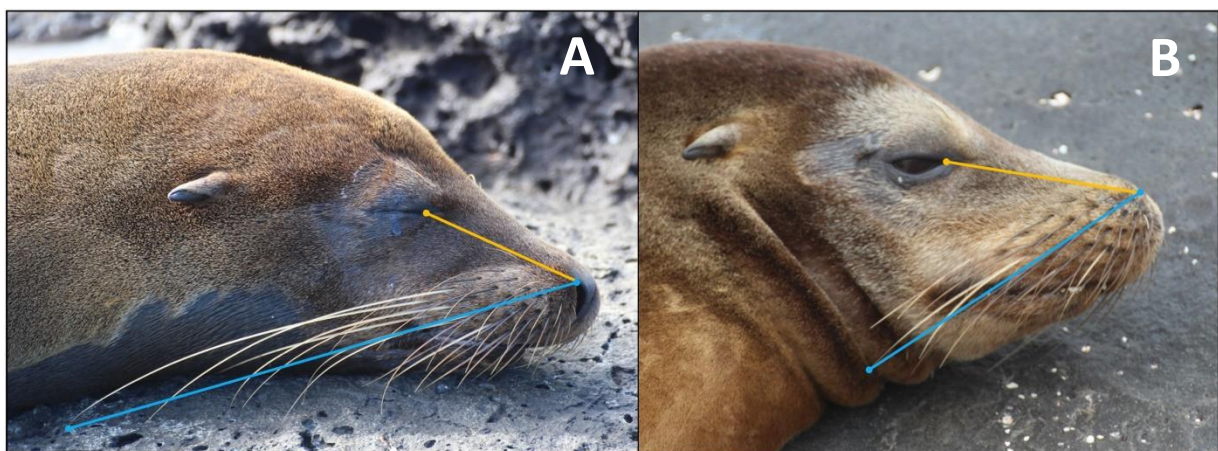
105 This study was carried out within a breeding colony of Galápagos sea lions (*Zalophus wollebaeki*) on
106 the islet of Caamaño, located near Santa Cruz Island in the centre of the Galápagos archipelago (0°45'
107 S, 90° 16' W). The colony has been monitored since 2003 and during annual field seasons, the birth and
108 growth of pups is documented, individuals are captured and tagged, and population census are carried
109 out (Trillmich et al., 2016). The vast majority of animals are individually marked with flipper tags
110 (Allflex®) and thereby recognizable, hence detailed life history data are available.

111 Dive data were collected on 34 lactating females with dependent offspring in the colony during the
112 reproductive seasons (October-December) of 2018 and 2019. Animals were captured using hoop nets
113 and biologgers (MK10, Wildlife Computers, Redmond, WA, USA) were attached to the dorsum for

114 approximately 2 weeks (median 15 days, range 3-22) before being removed again (see Jeglinski et al.,
115 2013 for more details). The loggers collect data on dive depth (every 2 seconds), GPS position through
116 fastloc-GPS (every 4 minutes) and acceleration data (32 hertz). Foraging strategies were established in
117 the previous publication by Schwarz et al. (2022) using an automated broken stick algorithm (Heerah et
118 al., 2014) and Hidden Markov Models. For further details of dive data collection and analysis, see
119 Schwarz et al. (2022).

120 **Measurement of relative vibrissae length**

121 Between 2019 and 2023, in a total of 7 field seasons (four reproductive (October – December) and three
122 non-reproductive (March-April) periods), photographs were taken of tagged females with their head in
123 profile and the tip of the longest vibrissae visible. This resulted in 476 images from 115 individuals
124 contributing to this study. Relative vibrissae length (RVL) was calculated as the ratio of the relative
125 distance (in pixels) from the upper point of the nostril opening to the tip of the longest vibrissae and the
126 relative distance (in pixels) from the upper point of the nostril opening to the *Caruncula lacrimalis* of
127 the eye (see Figure 1). To further our understanding of the potential life-stage dependency of vibrissae
128 length differences, we additionally photographed juvenile animals (1-4 years of age) starting in 2021.
129 This resulted in a dataset of 234 images from 96 juveniles sampled over six field seasons (four
130 reproductive, two non-reproductive). Images were processed and measured using the software GIMP
131 (The GIMP team, GIMP 2.10.32). The methodology is based on Schwarz et al. 2022.



132

133 **Figure 1.** Example images of females in profile with long (A) and short (B) vibrissae, illustrating the measurements
134 used to calculate relative vibrissae length. Orange: nostril opening to the eye. Blue: nostril opening to the tip of
135 the longest vibrissae. (Images by S. Stoehr)

136 **Relationship between foraging strategy and RVL**

137 For 32 adult females, RVL measurements as well as foraging strategy, previously determined by
138 Schwartz et al. (2022), were available. A linear model was used to analyse the relationship between
139 RVL and foraging strategy, including female age as additional explanatory variable.

140 To determine the threshold for RVL that differentiates benthic and pelagic foragers, we visually assessed
141 the distribution of RVL values. The RVL distributions of known benthic and pelagic foragers were
142 overlaid, and a threshold was selected at the point of minimal overlap between the two groups (Fig. S1).
143 Individuals with mean RVL above this threshold were assigned to the benthic foraging group, while
144 those below were classified as pelagic foragers. To evaluate the accuracy of this classification, we
145 compared the RVL-based group assignment to the known foraging strategy derived from dive data. This
146 classification approach based on RVL allows for inferring foraging strategies in individuals without
147 biologging data in future studies.

148 **Repeatability of RVL measurements**

149 All images were processed and RVL was measured by a primary observer. To test the intra-observer
150 reliability, a subset of one image of 83 adult females (reproductive period 2019) was re-measured by the
151 same observer six months after the initial measurements. This same subset was additionally measured
152 by two other observers to test for inter-observer reliability. Within and between observer repeatability
153 was tested using the R package rptR (Stoffel et al., 2017). The same package was used to test for within-
154 and between-season variability of RVL of both juvenile and adult individuals separately. Within-season
155 variability was tested for all individuals where two images within the same season were available, to
156 assess the reliability of the method across pictures. If an individual had repeated measurements from
157 multiple seasons, all were included (females: 154 repeat measurements on 115 individuals; juveniles:
158 168 repeat measurements on 81 individuals). For between-season repeatability, only individuals with
159 RVL measurements from at least two seasons were included, excluding repeat measurements within the
160 same season, resulting in 82 adult females with a total of 289 measurements and 34 juveniles with 85
161 measurements, respectively.

162 **Comparison of RVL across age groups**

163 To investigate whether differences in vibrissae length are exclusive to adults or are already detectable
164 at an earlier life stage, we compared mean RVL of juveniles and adult females from three separate
165 seasons with the largest sample sizes (autumn 2021: $n = 37$ juv, 63 fem; spring 2022: $n = 37$ juv, 53
166 fem; autumn 2022: $n = 23$ juv, 55 fem). To compare the variance and mean of RVL between juveniles
167 and adult females, we used a linear mixed model (LMM) fitted with restricted maximum likelihood
168 (REML). The model included life stage as a fixed effect and sampling season as a random effect to
169 account for potential inter-seasonal variation: $\text{RVL_mean} \sim \text{life stage} + (1|\text{season})$. A variance structure
170 allowed for different variances between groups. To test for differences in variance, we performed
171 Levene's test for homogeneity of variance.

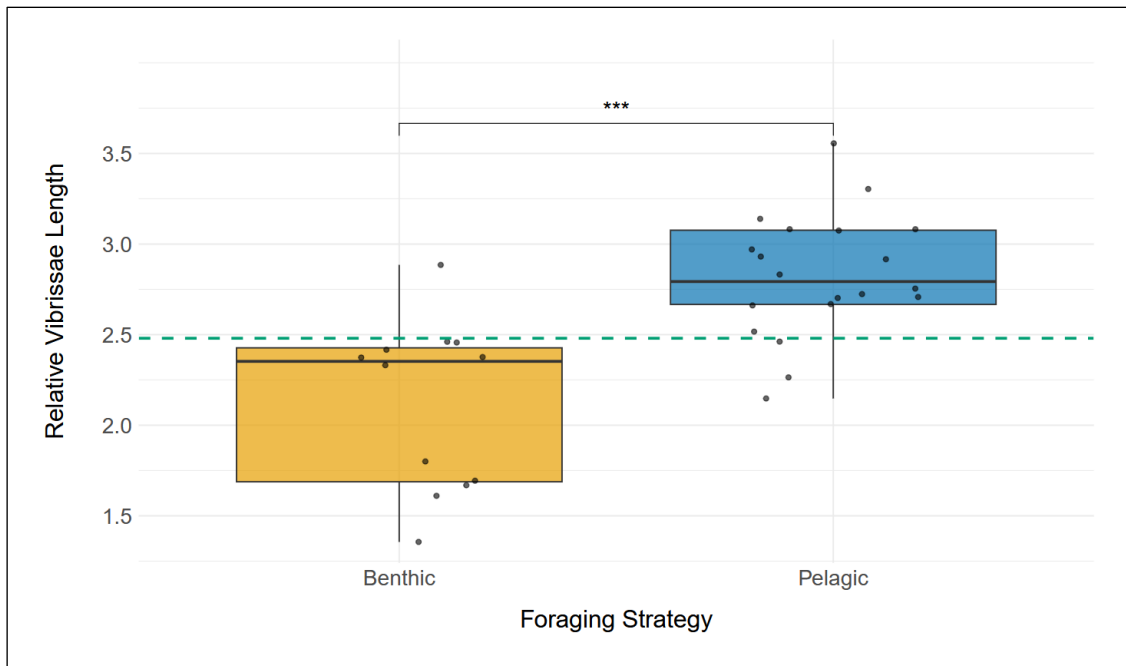
172 **RESULTS**

173 **Relationship between foraging strategy and RVL**

174 The linear model revealed a significant relationship between vibrissae length and foraging strategy
175 ($F_{(2,19)} = 13.31$, $R^2 = 0.584$, $p < 0.001$), with pelagic individuals showing higher RVL than benthic
176 individuals ($\beta = 0.69$, $p < 0.001$, Figure 2). Age was not a significant predictor ($\beta = 0.03$, $p = 0.163$).
177 The strong significant effect of foraging strategy remained when removing age from the model (see
178 Table S1).

179 The median RVL was 2.35 (IQR: 1.69–2.43) for benthic foragers ($n = 12$) and 2.79 (IQR: 2.67–3.08)
180 for pelagic foragers ($n = 20$). The IQRs of the two groups do not overlap, indicating a clear distinction
181 in the spread of RVL between the two foraging strategies, supporting the validity of classification based
182 on RVL. While benthic foragers show slightly greater variance in RVL values, there is no significant
183 difference in variability between the groups ($F_{(1,30)} = 1.28$, $p = 0.266$).

184 The comparison of RVL distributions between benthic and pelagic foragers indicated a threshold of 2.48
185 (benthic < 2.48 , pelagic > 2.48), representing the point of minimal overlap. Using this threshold, 28 of
186 the 32 females with known foraging strategies from biologgers were correctly classified using RVL,
187 resulting in an accuracy of 87.5%.



188

189 **Figure 2. RVL comparison of benthic (orange) and pelagic (blue) foragers (**p < 0.001).** Median, upper and
 190 lower quartiles are displayed and individual data points (n=32) are shown as black dots. The green dashed line
 191 indicates the RVL threshold (2.48) between the two groups.

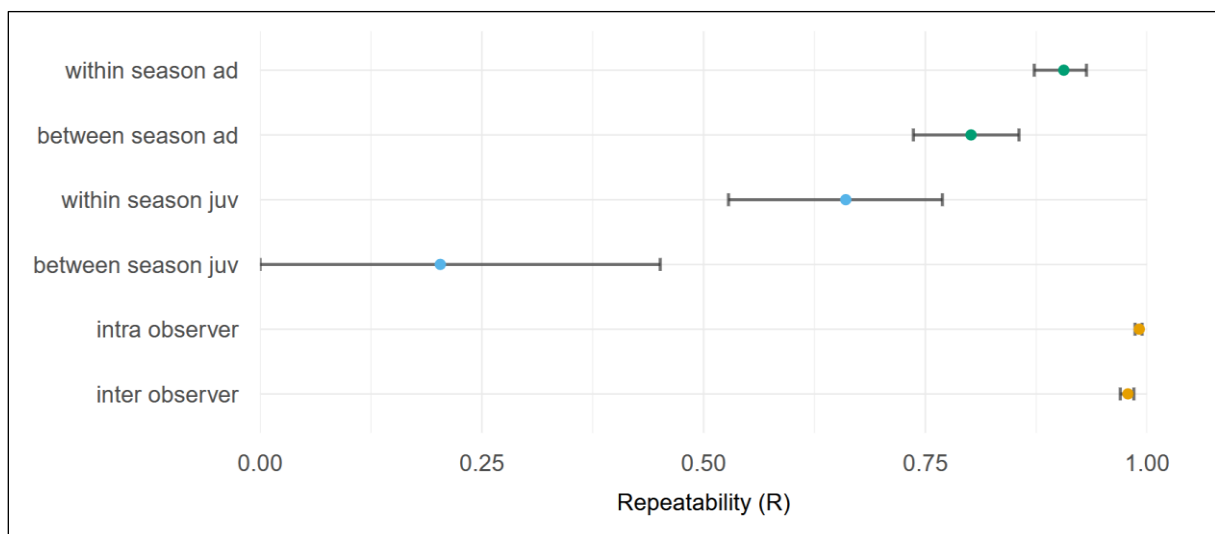
192 **Observer Reliability: Intra- and Inter-Observer Repeatability**

193 The intra-observer repeatability, assessed by the primary observer measuring the same images six
 194 months apart, was high (R = 0.99, 95% CI: [0.987, 0.994], SE = 0.002). Similarly, inter-observer
 195 repeatability, based on measurements from three different observers, was high as well (R = 0.98, 95%
 196 CI: [0.968, 0.985], SE = 0.004). Both results were highly significant according to the likelihood ratio
 197 test ($P_{intra} = 6.41e-75$, $P_{inter} = 6.4e-120$) and the permutation test (P = 0.001). These findings confirm that,
 198 once properly established and standardized, the method remains highly reliable and repeatable across
 199 different observers.

200 **Repeatability of RVL measurements across seasons and age groups**

201 Overall, RVL measurements are highly repeatable in adult females, whereas juveniles exhibit markedly
 202 lower stability (Figure 3). Repeatability estimates for RVL were assessed both within and between
 203 seasons. For adult females, within-season repeatability was very high (R = 0.91, 95% CI: [0.873, 0.931],
 204 p < 0.001), demonstrating a strong reliability of the methodological approach. While the within-season
 205 repeatability validates the methods, the high between-season repeatability (R = 0.80, 95% CI: [0.730,
 206 0.856], p < 0.001) demonstrates the stability of RVL in females over multiple years, indicating that RVL

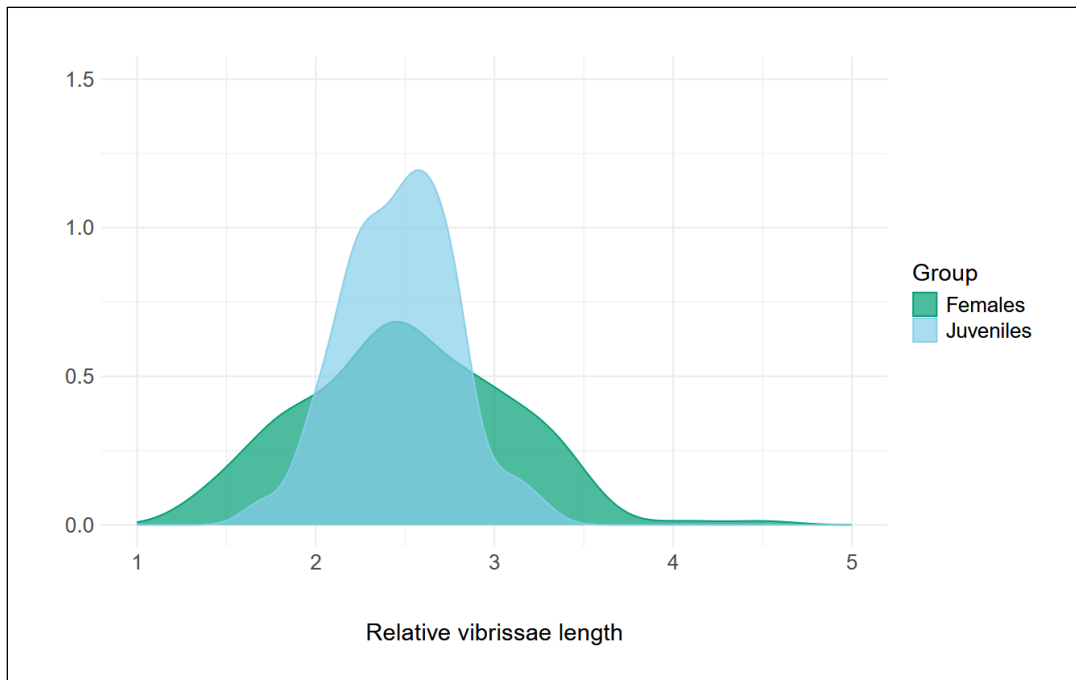
207 is a stable trait. In contrast, the repeatability of RVL in juveniles was considerably lower, with moderate
208 within-season repeatability ($R = 0.66$, 95% CI: [0.52, 0.763], $p < 0.001$), and low between-season
209 repeatability ($R = 0.20$, 95% CI: [0, 0.452], $p = 0.047$) with overall wider confidence intervals. These
210 results suggest that the reliability of the methodological approach is not as high in juveniles as it is in
211 adult females. The considerable low repeatability between seasons on the other hand, together with the
212 wider confidence intervals, demonstrate a lack of RVL stability in juvenile sea lions in their first years.



213
214 **Figure 3: Repeatability estimates of RVL measurements** in adult females (green) and juveniles (blue) within
215 and between sampling seasons; and for method validation through intra- and inter-observer checks (orange).
216 Horizontal error bars indicate 95% confidence intervals.

217 Comparison of RVL across age groups

218 The linear mixed model revealed that mean RVL did not differ significantly between juvenile and adult
219 females ($\beta = -0.042$, $SE = 0.054$, $t(264) = -0.79$, $p = 0.43$). However, the variance in mean RVL between
220 the two groups differed significantly, with adult females showing greater variability (variance ratio =
221 1.85; Levene's test: $F = 30.79$, $p < 0.0001$). This suggests that while the mean vibrissae length is similar
222 across life stages, adult females exhibit a wider range of RVL (Figure 4), reflective of individual
223 behavioural differences in foraging as described above. Season had no detectable effect on RVL
224 (random effect variance = $1.85e-05$). These results indicate that individual differences in RVL persist
225 across time, confirming the stability of the observed variation and the robustness of RVL as a foraging-
226 related trait.



227

228 **Figure 4.** Density distribution of mean RVL of juveniles (blue) and adult females (green).

229 **DISCUSSION**

230 Our analysis confirmed that individual differences in vibrissae length are linked to distinct foraging
 231 strategies in Galápagos sea lions. Moreover, RVL remained stable across multiple years, indicating long-
 232 term persistence in individual foraging specialization. We also found that this morphological
 233 polymorphism is not detectable in juveniles, suggesting that foraging specializations develop primarily
 234 in adulthood.

235 **Vibrissae length reflects foraging strategy**

236 We could confirm that vibrissae length differences observed within the population are not merely
 237 random phenotypic variation but instead reflect the distinct foraging strategies that have been established
 238 for GSL (Schwarz et al., 2022; Villegas-Amtmann et al., 2008). Specifically, the significantly shorter
 239 vibrissae observed in benthic foragers are likely the result from increased abrasion that is found within
 240 this foraging strategy. Dietary studies have shown that GSL of this colony frequently prey on burrowing
 241 cusk-eels (*Chilara taylori* and *Otophidium indefatigable*, Páez-Rosas & Aurióles-Gamboa, 2014),
 242 which requires the sea lions to dig within the substrate. This is further supported by body pitch data from
 243 biologgers, indicating that benthic foragers regularly orient their bodies toward the sea floor (Schwarz

244 et al. 2022). Over time, this consistent higher level of abrasion at the snout results in shorter vibrissae
245 that distinguishes benthic from pelagic foragers, who experience considerably lower levels of abrasion
246 hunting in the open water column. Using vibrissae length as a morphological proxy to classify females
247 into foraging strategies showed high accuracy, as 87.5% of females were put into the same strategy as
248 identified by dive analysis. However, a small number of individuals were misclassified, as animals with
249 intermediate RVL values may be more difficult to categorize compared to individuals from the ends of
250 the RVL spectrum. This highlights the importance of assessing how reliably vibrissae length differences
251 can be measured using RVL derived from photographs.

252 **Reliability of RVL**

253 When testing the reliability of measuring RVL with photographs, both the effect of the different images
254 and angles, as well as the human component, must be considered. The high repeatability of RVL
255 measurements within season ($R = 0.91$) as well as the exceptionally high intra- and inter-observer
256 repeatability ($R = 0.99$ and $R = 0.98$) address these concerns respectively and demonstrate the accuracy
257 and reproducibility of this method. The high within-season repeatability further suggests that a single
258 well-taken image per individual can provide a reliable estimate of RVL, making the method highly
259 suitable for large-scale data collection. To minimize measurement error, images should be taken in
260 perfect profile, as angle distortions could artificially alter the apparent length of the vibrissae and reduce
261 measurement accuracy (Sadou et al., 2014). However, with proper standardization, RVL measurement
262 could potentially even be automated, as seen in other studies utilizing machine learning for image-based
263 data extraction (Gray et al., 2019; Kühn & Burghardt, 2013).

264 The more moderate within-season repeatability of RVL in juveniles suggests that this approach is not
265 universally effective. Given the slow rates of vibrissae growth and abrasion, significant within-season
266 changes in RVL are unlikely. Instead, the lower repeatability in juveniles likely stems from reduced
267 between-individual variability. Since repeatability depends on the ratio of within-individual to between-
268 individual variation, lower diversity among juveniles decreases repeatability, even if measurement error
269 and individual vibrissae length remain stable. In contrast, the greater between-individual variation in
270 females enhances their repeatability, making RVL a reliable marker for foraging strategies in this group.

271 **Benefits & limitations of RVL-based classification**

272 Having established the reliability of RVL as a proxy for foraging strategy, it is important to consider
273 both advantages and limitations of this approach. A key benefit of RVL-based classification is its non-
274 invasive nature, allowing for data collection from a distance using images rather than requiring direct
275 handling of the animals. In contrast, traditional biologging studies on pinnipeds and other wild animals
276 require capture, and in some cases sedation, for device attachment, sometimes requiring a second capture
277 for retrieval. While best-practice protocols exist for the use of telemetry devices on pinnipeds (Horning
278 et al., 2019; Wilson & McMahon, 2006), extended and repeated handling can induce stress with potential
279 negative consequences (Champagne et al., 2012; Cooley et al., 2025; Harcourt et al., 2010). RVL
280 measurements, however, can be obtained remotely, minimizing disturbance while also reducing
281 logistical constraints. While biologging technology continues to advance and becomes more accessible
282 (Chung et al., 2021; Wilmers et al., 2015), it still involves significant costs and logistical efforts. In
283 contrast, RVL assessment requires only a camera, making it a cost-effective alternative, and allowing
284 for significantly higher sample sizes due to its simplicity. Another major advantage of this method is its
285 suitability for longitudinal studies, as individuals can be photographed repeatedly over time. This
286 facilitates long-term monitoring of foraging strategies, enabling researchers to track behavioural shifts
287 across life stages or in response to changing environmental conditions.

288 However, the accuracy of the RVL method depends on prior knowledge of foraging behaviour, as RVL-
289 based classification relies on validation from biologging data. Without such reference datasets,
290 distinguishing foraging strategies solely from vibrissae length would be invalid. Furthermore, unlike
291 biologgers, which can provide fine-scale data on movement, physiological and environmental
292 parameters (Chung et al., 2021; Watanabe & Papastamatiou, 2025), RVL classification offers only a
293 broad behavioural categorization and lacks detailed insights into individual foraging strategies. Another
294 limitation is the requirement for uniquely identifiable individuals, as tracking changes over time
295 necessitates consistent re-identification of the same animals. Further, the method's effectiveness relies
296 on the ability to obtain high quality, reliable photographs, which may be challenging for more cryptic
297 species or ones not as habituated to human presence. While the limitation of indirectly measuring

298 vibrissae length through photographs, rather than directly, is inherent to the non-invasive nature of the
299 method, careful standardization of image collection protocols will contribute to maintain reliability.

300 **Significance of morphological indicators**

301 Morphological traits have long been recognized as indicators for foraging behaviour in animals (Grant
302 et al., 1985; Kay, 1984). Typically, such traits arise through evolutionary processes at the species level
303 as adaptations to diet (Fenton & Bogdanowicz, 2002; Hulseley & García De León, 2005; Moermond &
304 Denslow, 1985). However, in some cases, morphological changes occur within an individual's lifetime
305 and remain stable over extended periods, reflecting consistent behavioural patterns. A well-documented
306 example is the Eurasian Oystercatcher (*Haematopus ostralegus*), where specialized feeding behaviours
307 in prey selection and handling lead to distinct bill shapes due to abrasion (Swennen et al., 1983; Van De
308 Poll et al., 2009). Similarly, studies on freshwater fish have shown that body morphology can shift in
309 response to resource availability and diet (Andersson et al., 2005; Hjelm et al., 2001). In those examples
310 where morphological differences arise within a lifetime, diet often influences morphology rather than
311 the other way around. While some morphological adaptations serve a clear functional role, such as
312 optimized foraging efficiency through adapted jaw shape in sunfish *Lepomis humilis* (Hegrenes, 2001),
313 the abrasion-induced shortening of vibrissae in sea lions appears non-functional. This raises the
314 possibility that similar morphological proxies might exist in other species, potentially being overlooked,
315 as they do not seem to serve an obvious functional purpose. Vibrissae length as an indicator of foraging
316 behaviour may be applicable to other pinniped species besides Galápagos sea lion. Vibrissae abrasions
317 in general have been observed in some species, including Weddell seals (*Leptonychotes weddellii*) and
318 New Zealand sea lions (*Phocarctos hookeri*) (D. Costa, L. Chilvers, pers. communication). More
319 broadly, abrasion-related indicators could exist in other taxa, highlighting the need for broader
320 exploration of morphological traits as behavioural proxies.

321 **Biological implications of foraging specialization**

322 Beyond establishing a novel morphological proxy, our findings provide biological insights into the long-
323 term stability of foraging strategies in GSL. RVL measurements remained stable across multiple years
324 ($R = 0.80$), despite vibrissae being a continuously growing structure. Otariids do not shed their vibrissae

325 (Cherel et al., 2009) and while growth rates are known to vary by age and sex, they are estimated at 0.1
326 ± 0.05 mm per day (*Z. californicus*, Rosas-Hernandez et al., 2018), which would translate to
327 approximately 3.5cm per year and could significantly change RVL. However, the observed stability of
328 RVL values across multiple sampling seasons and years suggests that vibrissae abrasion patterns, shaped
329 by foraging strategy, are maintained. This level of stability has not been previously described for GSL,
330 with individuals keeping their vibrissae length and thus their foraging strategy throughout the
331 measurement period (3.5 years) and likely beyond.

332 In addition, our results indicate that specialization into distinct strategies, reflected by stable RVL, is
333 found primarily in adulthood. Juveniles exhibit a narrower RVL distribution, despite having similar
334 mean values to adults, and show low repeatability of RVL across seasons ($R = 0.20$). This suggests that
335 the foraging behaviours affecting vibrissae length are not yet established during those early stages of
336 life. These findings align with previous studies showing that once juvenile GSL start foraging
337 independently, they often occupy distinct foraging niches that do not overlap with those of adults
338 (Jeglinski et al., 2012). However, it appears that once individuals specialize into benthic or pelagic
339 strategies as adults, they maintain those consistently over time.

340 Foraging specializations have been widely documented across taxa (Ceia & Ramos, 2015; Sheppard et
341 al., 2021; Toscano et al., 2016) and specifically in pinnipeds (Baylis et al., 2015; Kernaléguen et al.,
342 2015; Seguel et al., 2022). Specialization can enhance foraging efficiency and reduce intraspecific
343 competition. However, it may also increase vulnerability to environmental change, as specialists are less
344 adaptable when resources fluctuate (Araújo et al., 2011; Bolnick et al., 2003; Sargeant, 2007).
345 Understanding the long-term stability and ecological consequences of such specializations is therefore
346 essential for assessing population resilience under changing environmental conditions.

347 **Conclusion**

348 This study establishes RVL-based classification from images as a valuable tool for large-scale
349 assessment of foraging strategies in adult female GSL, and potentially other pinnipeds. It provides new
350 insights into the development and persistence of individual foraging specialization, offering a non-
351 invasive and cost-effective method to study behaviour at the population level. While biologgers remain

352 indispensable for detailed behavioural analyses, integrating RVL measurements with existing tracking
353 methods could allow researchers to balance precision with scalability, ultimately improving our
354 understanding of individual specialization and population-level foraging dynamics. Beyond pinnipeds,
355 our findings highlight the potential for morphological traits to serve as indicators of behavioural
356 polymorphisms. This underscores the broader importance of studying behaviour at an individual level -
357 not only to understand species ecology but also to better predict responses to environmental changes.

358

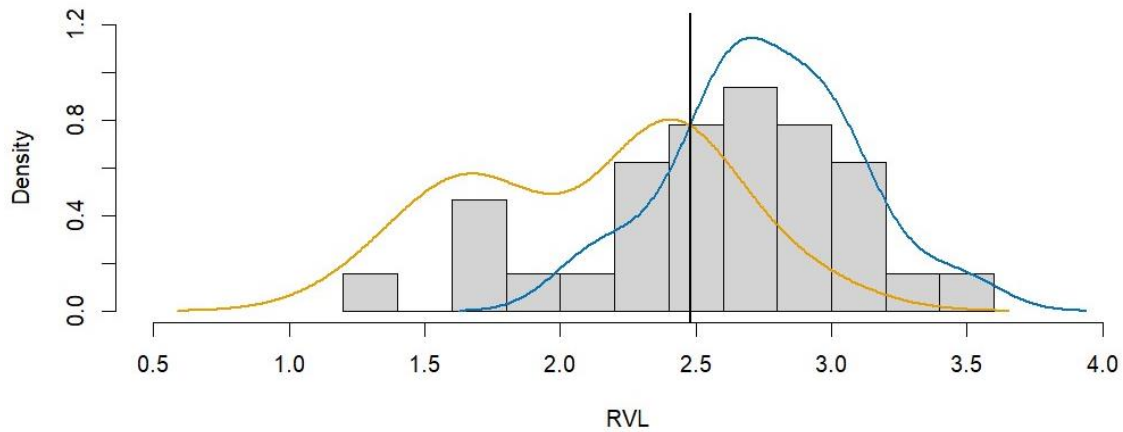
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367 The authors declare no conflict of interest.

368 **Supplementary material:**



369

370 **Figure S1.** RVL distribution of benthic (orange) and pelagic (blue) foragers and the selected threshold value of
 371 2.48 at the point of minimal overlap between the two groups.

372

<i>Predictors</i>	Exact age (F (2,19) = 13.31)				Weak age (F (2,22) = 8.43)			Age excluded (F (2,30) = 24.35)		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	<i>Estimates</i>	<i>CI</i>	<i>p</i>	
(Intercept)	-63.32	-157.60 – 30.96	0.325	-57.84	-156.00 – 40.33	0.436	2.12	1.89 – 2.35	<0.001	
group [1]	0.69	0.39 – 0.99	<0.001	0.59	0.28 – 0.90	0.002	0.71	0.41 – 1.00	<0.001	
cohort e	0.03	-0.01 – 0.08	0.325							
cohort w				0.03	-0.02 – 0.08	0.436				
Observations	22			25			32			
R ² / R ² adjusted	0.584 / 0.540			0.434 / 0.382			0.448 / 0.430			
AIC	15.733			23.582			34.741			

373

374 **Table S1: Model comparison.** Linear model for the relationship between RVL and foraging strategy. Model 1
 375 and 2 include age as explanatory variable. Model 1 only includes animals with exact birth cohort data, while model
 376 2 includes those with birth year known within ±1 year. Benthic foragers serve as the reference group and group
 377 [1] represents pelagic foragers. Reported p-values are adjusted using Holm's correction to control for multiple
 378 testing.

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