BEHAVIORAL INSIGHTS INTO THE GALAPAGOS PENGUIN *SPHENISCUS MENDICULUS*: A DAY IN HIS LIFE—AN ETHOLOGICAL PORTRAIT

JONATHAN CUEVA[1], WILSON IÑIGUEZ[1], GREGORY MARSHALL[2], CHRISTIAN SEVILLA[3], ANDREA COLOMA[1], LORENA VENEGAS[1], & GUSTAVO JIMÉNEZ-UZCÁTEGUI[1]*

[1]*Charles Darwin Research Station, Charles Darwin Foundation, Puerto Ayora, Galápagos, Ecuador *(gustavo.jimenez@fcdarwin.org.ec)*
[2]*National Geographic – Remote Imaging, Washington, DC, USA*
[3]*Galápagos National Park Directorate, Puerto Ayora, Galápagos, Ecuador*

Received 1 August 2025, accepted 21 November 2025

ABSTRACT

Cueva, J., Iñiguez, W., Marshall, G., Sevilla, C., Coloma, A., Venegas, L., & Jiménez-Uzcátegui, G. (2026). Behavioral insights into the Galapagos Penguin *Spheniscus mendiculus*: A day in his life—an ethological portrait. *Marine Ornithology*, *54*(1), 177–183. http://doi.org/to come...

The Galapagos Penguin *Spheniscus mendiculus*, endemic to the Galápagos Archipelago, faces increasing ecological pressures threatening its population. This study aimed to characterize its daily behavioral patterns to better understand its adaptations and vulnerability to ecosystem changes. In one breeding locality, the Marielas Islets, we mounted a Crittercam on a male penguin to assess interactions with its mate and its behavior over a 24-hr period. Behaviors were classified as Diving, Foraging, Grooming, Intraspecific Interaction, Interspecific Interaction, Loafing, Prospecting, Resting, Surface Dipping, and Swimming. We analyzed behavioral data using chi-square tests and transition heat-maps. Results revealed predominantly surface behaviors—Prospecting (41.2% of observed time) and Surface Dipping (38.4%)—with deep diving and socializing being rare (< 10%). Significant behavioral transitions ($P < .001$) included a strong association between Swimming and Diving, suggesting a structured foraging strategy. Activity durations varied diurnally, with peak surface behaviors occurring during daylight. These patterns indicate behavioral adaptation to prey availability. Although we had data from just one individual, the low frequency of deep diving was unexpected and contrasts with findings for other penguin species. Our findings provide insight into factors affecting foraging success for the Galapagos Penguin. We recommend expanded monitoring with a larger sample of Crittercams to evaluate behavioral patterns that could facilitate conservation strategies.

Key words: behaviors, Crittercam, ethology, foraging ecology, Sphenisciformes

INTRODUCTION

The Galapagos Penguin *Spheniscus mendiculus* (GAPE) faces increasing ecological pressures that threaten its population, while also being the only penguin species that copes with the equatorial region (Harris, 1973; Jiménez-Uzcátegui, 2022). Endemic to the Galápagos Archipelago, 95% of the population lives on two islands, Fernandina and Isabela, with small populations also at Bartolomé, Floreana, and Santiago (Harris, 1974; Vargas, 2006). This penguin is adapted to tropical conditions on land but inhabits a temperate marine environment similar to those of other low-latitude penguins such as the Humboldt Penguin *S. humboldti* and the African Penguin *S. demersus*. This combination sharply distinguishes it from its relatives in temperate and polar regions (Acosta Hospitaleche, 2005).

The Galápagos Archipelago is of volcanic origin and, though located at the Equator, is surrounded by cool, nutrient-rich waters due to the upwelling associated with the convergence of four currents: Humboldt, Cromwell, Ecuadorian, and Panama (Ainley & Wilson, 2023; Bjerknes, 1969; Karnauskas et al., 2015). Owing to a highly variable ocean climate influenced by the El Niño Southern Oscillation (ENSO), prey availability for this generalist and opportunistic species can fluctuate considerably. Its breeding success depends on periods of abundant small pelagic fish (Boersma, 1976; Boersma et al., 2013; Mills, 1998; Steinfurth, 2007; Vargas, 2006). GAPE forages nearby at shallow depths, ranging from 15 to 50 m deep (Steinfurth et al., 2008; Vargas et al., 2006).

The GAPE tendency to forage primarily in shallow waters suggests that doing so is energy-efficient, adequate, and associated with Cromwell Current upwelling (Ruiz & Wolff, 2011). Their daily routine follows a consistent pattern: leaving the nest at dawn (05h00–05h30), resting on land mid-morning (10h00–11h30), and returning to the nest by late afternoon (17h45) (GJU, personal observations; Jiménez-Uzcátegui & Vargas, 2019; Steinfurth, 2007).

Directly studying the feeding behavior of marine species that hunt underwater is challenging due to the inaccessibility to humans of their environment, the depths they reach, and technological limitations for real-time observation (Karnauskas et al., 2015; Viviant et al., 2014). However, recent advances in tracking technologies have begun to overcome several of these limitations (Marshall et al., 2007). These indirect methods have been essential for defining ecological niches and food interactions, helping us to understand how species use available resources, as seen in other penguin species (Lynnes et al., 2002; Miller et al., 2010; Trivelpiece et al., 1987). This study aims to understand how a GAPE individual allocates its behavior throughout the day, mostly related to time in the water.

METHODS

Study Area

The study was carried out on the Marielas Islets, comprising the East, South, and North islets, located in the western portion of the Galápagos Archipelago, approximately 960 km from the coast of mainland Ecuador. The GAPE captured was from Mariela East (00°35′40.70″S, 091°05′25.1″W; Fig. 1; Snell et al., 1996).

Crittercam Placement

A Crittercam system (an integrated video device designed to study the behavior of animals in their natural habitats; see Marshall, 1998; Marshall et al., 2007) was attached to the back of a GAPE. This was done using a custom harness made of flexible and lightweight materials to ensure a secure attachment and minimize any potential discomfort or interference with the penguin's movements. The harness included an easy-release mechanism that enabled quick removal of the device, minimizing both stress and the risk of injury. The physical condition and behavior of the GAPE were continuously monitored throughout the placement process to detect any signs of stress or discomfort, thereby ensuring its welfare at all times.

The study focused on a nesting adult male GAPE (approx. 4 years old), which was captured and equipped with the Crittercam on 10 November 2016. For long-term identification within the capture–recapture program at Charles Darwin Foundation, the individual had been previously marked with a microchip (9810981045-33600) on 18 July 2016. Notably, it was subsequently recaptured several times (15 July 2017, 26 July 2018, and 18 August 2019), allowing for data retrieval and health assessments. As a breeding adult with a chick, its behavior was expected to reflect provisioning strategies, providing insights into its foraging efficiency and interactions within the marine environment.

Data Analysis

This study is based on data collected from a GAPE monitored with a Crittercam. The device was deployed on 10 November 2016 at 18h00 and retrieved 24 hr later, on 11 November 2016 at 18h00. This deployment schedule enabled continuous monitoring beginning at dawn (05h00) on 11 November, when the species initiates its daily activity. As such, the dataset represents the behavior of one individual on one day and should be interpreted as an exploratory case study. Prior to analysis, two researchers independently reviewed the video footage to identify and classify observed behaviors. Based on this process, a reference framework was established for the construction of the ethogram. Behavioral categorization followed the principles of classical ethology (see Eibl-Eibesfeldt, 1975, 2012). The functional ethogram we developed included the following behaviors (see Table 1 for definitions): Diving, Foraging, Grooming, Intraspecific Interaction, Interspecific Interaction, Loafing, Prospecting, Resting, Surface Dipping, and Swimming. We analyzed the timing of each behavior, allowing us to identify the individual's priorities, adaptive strategies, and behavioral transitions. Subsequently, detailed analysis was carried out using BORIS v.2.8 software (Friard & Gamba, 2016), dedicating 1–1.5 hr to the review of each video, depending on the complexity of the interactions and the duration of the recorded behaviors.

Statistical Analysis

The Crittercam produced 12 video clips of approximately 20 min each. However, the files did not contain precise metadata indicating the exact start and end times of each segment, and recording was not continuous. For the analyses, we assumed that the video clips were consecutive and followed the order in which they were recorded. The recorder began operating at 06h00 on 11 November 2016, according to the device's programmed ignition schedule, which approximates the expected start time in the absence of exact metadata. This assumption allowed us to organize the data into time

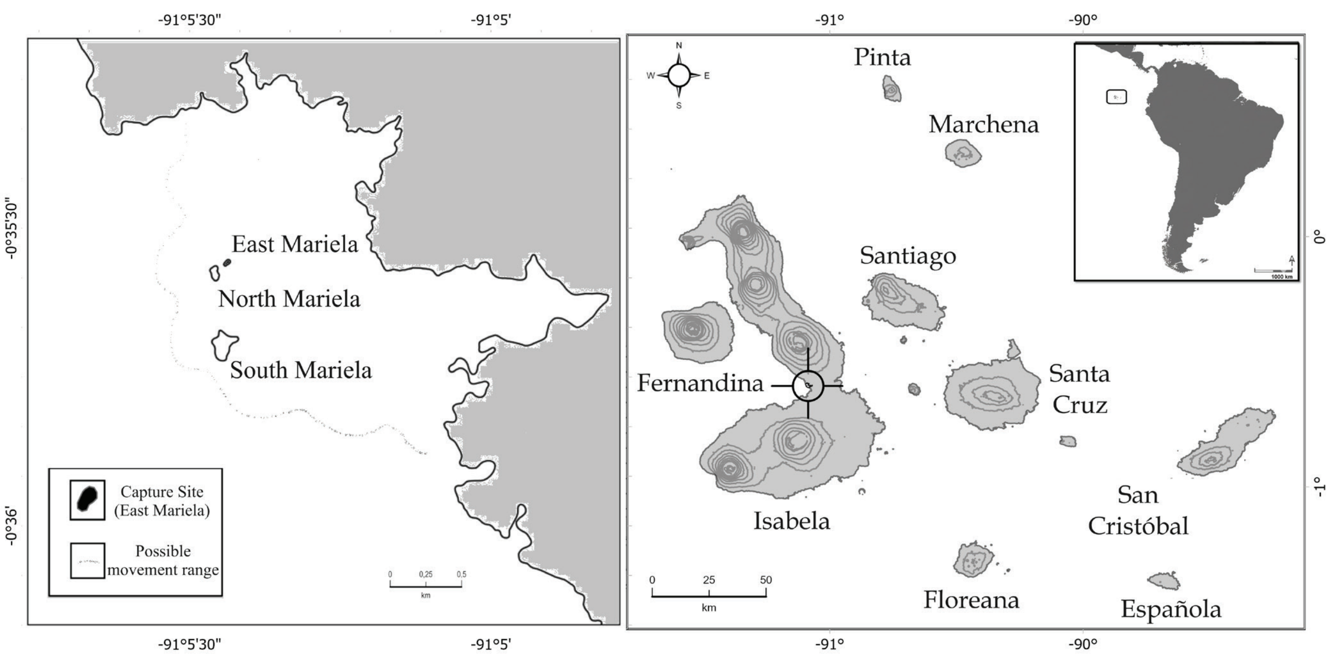

Fig. 1. The rectangle inset at top right shows the Galápagos Islands within a rectangle. The right-hand panel displays the archipelago, with a symbol indicating the location of the Marielas islets. The left-hand panel illustrates the capture site and the possible movement range of the Galapagos Penguin *Spheniscus mendiculus* (GAPE) studied. The capture took place on East Mariela Islet, off the western coast of Isabela Island.

TABLE 1
Galapagos Penguin *Spheniscus mendiculus* ethogram classified by type and event category recorded by Crittercam

Behavior	Code	Definition
Diving	DV	Penguin completely submerges for > 1 s
Foraging	FR	Active pursuit and capture of prey, usually involving repeated dives or underwater chases
Grooming	GR	Preening or feather maintenance
Interspecific Interaction	ID	Interaction with non-penguin species
Intraspecific Interaction	IS	Interaction between two or more penguins
Loafing	LF	Minimal movement, floating or standing
Prospecting	PP	Penguin scans, changes direction, without capturing prey
Resting	RT	Motionless penguin, eyes closed or relaxed posture
Surface Dipping	SD	Shallow immersion of head/upper body below the surface without a full dive
Swimming	SW	Continuous forward movement on the water surface

bins for analysis, but the temporal distribution of behaviors should be interpreted with caution, given these limitations.

Statistical analyses were performed using the RStudio software (RStudio Team, 2020) to provide the distribution and transition of the observed behaviors. A chi-square test was applied to determine whether the frequency of the behaviors differed significantly and to assess whether the individual distributed its time evenly among them.

The significant transitions between behaviors were calculated using frequencies (Table 2). To compare the duration of different behaviors, we applied Dunn's test to evaluate significant differences among them. Finally, we generated a transition diagram to visualize the relationships between behaviors and facilitate the interpretation of behavioral sequences (RStudio Team, 2020).

TABLE 2
Transition probability matrix describing the likelihood of sequential behaviors in the observed Galapagos Penguin *Spheniscus mendiculus* individual

Behavioral codes[a]	DV	FR	GR	ID	IS	LF	PP	SD	SW
DV	0	0.02	0	0	0.03	0	0.1	0.34	0.51
FR	0.23	0	0	0.01	0.03	0	0.56	0.09	0.07
GR	0.02	0	0	0	0	0.23	0	0.75	0
ID	0.2	0	0	0	0.4	0	0.2	0.2	0
IS	0.12	0.02	0	0	0	0	0.38	0.41	0.06
LF	0	0	0.75	0	0	0	0	0.25	0
PP	0.42	0.23	0	0	0.15	0	0	0.19	0
SD	0.29	0.01	0.06	0	0.12	0.01	0.14	0	0.37
SW	0.13	0.01	0.01	0	0.02	0	0.36	0.48	0

[a] For behavioral codes, see Table 1. Codes listed in the first column refer to the initial behavior, and codes listed across the columns refer to the subsequent behavior observed. Behaviors are presented in alphabetical order, following Table 1, and do not reflect the sequence of occurrence.

RESULTS

The behavioral repertoire described here corresponds to the activity of a single adult male GAPE during a 24-hr monitoring period. As such, the analysis is not replicated, and the results should be interpreted as preliminary insights into GAPE daily activity rather than population-level patterns. A total of 12 video clips of 20 min each were available. While this totaled 4 hr of footage, the effective recording time totaled 3 hr, 19 min, and 30 sec, the difference being due to interruptions and technical issues. Since the files lacked timestamps, the hourly distribution of behaviors should be interpreted as an approximate analytical framework. For consistency, the data were organized into one-hour intervals (06h00–10h00), used solely as a framework to facilitate comparisons. In practice, the sampling effort extended across daylight hours throughout the deployment. The behaviors considered in this analysis correspond to those defined in Table 1, with each coded and followed accordingly to ensure clarity and reproducibility.

The results showed that, when in the water, the individual's most frequent and predominant behaviors were Prospecting as the dominant activity, accounting for 41.2% of total time, followed by Surface Dipping (38.4%). These two activities make up most of the individual's behavioral repertoire, followed by Swimming (7%) (Fig. 2). While Resting is an established behavior in GAPE and was included in the ethogram (Table 1), it was not observed in this study, likely due to the limited recording duration and its occurrence during non-recording periods.

A chi-square test revealed highly significant differences in the distribution of behaviors ($P < .001$), indicating that the individual did not allocate time evenly across activities—i.e., certain behaviors were favored over others. Based on these results, we identified key patterns, including frequent, unlikely, and nonsignificant transitions. Among the most likely transitions, Swimming was often followed by Diving, Grooming by Loafing, and Foraging by Prospecting. Based on these observations, we quantified the probabilities of behavioral transitions and constructed a transition matrix (Table 2). These results demonstrate a structured temporal organization in the individual's activities.

Looking at the differences in the duration of the behaviors, assessed using the Dunn's test with Bonferroni correction, revealed two comparisons with significant differences: Interspecific

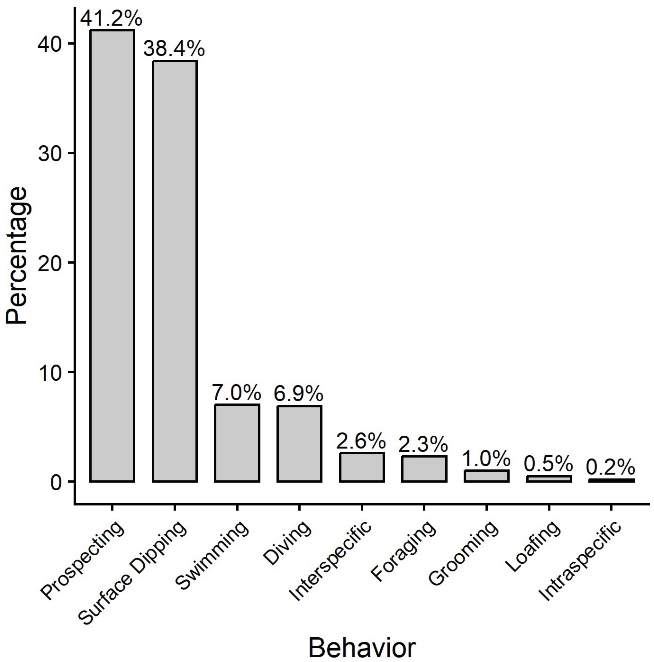

Fig. 2. Percentage of time spent in different behaviors by the breeding adult male Galapagos Penguin *Spheniscus mendiculus* (GAPE) observed at Mariela East Islet, Galápagos. For definitions of behaviors, see Table 1. Resting is omitted because the individual was not recorded in this state.

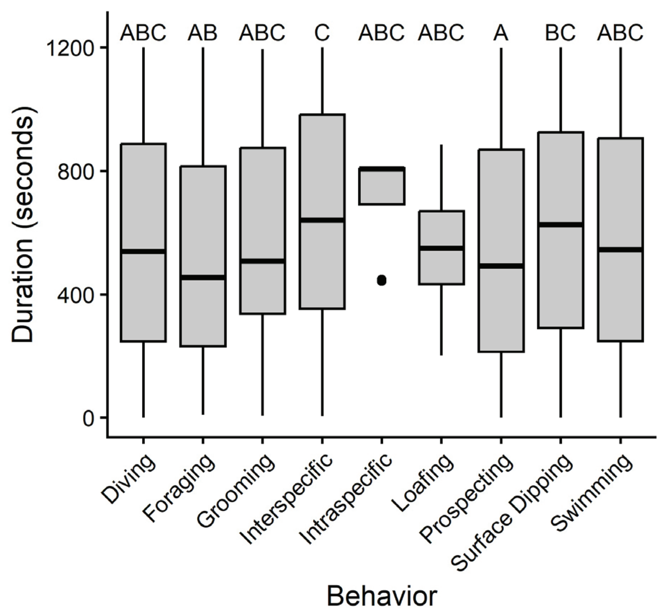

Fig. 3. Behavior groupings for observations of an adult male Galapagos Penguin *Spheniscus mendiculus* (GAPE) based on average duration according to post hoc tests. Three general groups of behavior were evident (indicated by letters), with some overlap. Behaviors are labeled with letters (A, B, C) that indicate statistical groupings: behaviors sharing one or more letters (e.g., "A," "AB," and "ABC") show no significant differences from each other, while behaviors with no shared letters (e.g., "A" and "BC") indicate statistically significant differences in duration. Box plots show the median (horizontal line), interquartile range (box), and range (whiskers).

Interaction vs. Prospecting ($P = 0.002$) and Prospecting vs. Surface Dipping ($P < .001$). Post hoc analysis using Dunn's test with Bonferroni correction identified significant differences ($P < .05$) in mean duration among key behaviors (Fig. 3). Three general groups emerged, indicated by letter assignments where behaviors sharing the same letter show no significant differences from each other, while behaviors differing in letters indicate statistically significant differences. Prospecting (labeled "A") was statistically distinct from Interspecific Interactions and from Surface Dipping, the only categories not sharing an "A" label. The Interspecific Interactions category (labeled "C") was statistically distinct from Foraging as well as from Prospecting, the only categories not sharing a "C" label. Foraging ("AB") and Surface Dipping ("BC") occupied intermediate positions, sharing statistical similarities with adjacent groups and potentially serving as behavioral transitions. This labeling system clarifies which behaviors have significantly different durations and facilitates interpretation of temporal patterns.

To complement the interpretation of temporal dynamics, we constructed a behavioral transition diagram (Fig. 4). This visualization represents the flow and frequency of transitions between behavioral states, highlighting the most common routes and indicating how intermediate behaviors, such as Foraging and Surface Dipping, can function as bridges in the overall sequence of activities.

DISCUSSION

This study served as a proof of concept for the use of Crittercam technology, which was deployed on a single GAPE for an assembled 24-hr monitoring period (10–11 November 2016) to describe fine-scale behavior. Given the exploratory nature and limited sample size ($n = 1$), the main objective was to demonstrate the methodological potential of these video systems to obtain detailed behavioral data, rather than to draw population-level inferences. Within this individual context, the analysis revealed specific behavioral patterns characterized by exploratory activity and frequent foraging, with passive behaviors occurring at low frequencies (see Table 1; Figs. 3, 4). This observed "daily routine," consisting of multiple short foraging trips, may represent an adaptive strategy to maximize food intake while minimizing time away from the nest during periods of high energetic demand, particularly during breeding (Boersma, 1976).

The results not only provide a detailed view of individual behavior but also highlight the usefulness and potential of the methodology employed. The Crittercam yielded both qualitative and quantitative data that complement and enrich traditional metrics for studying animal behavior (Eibl-Eibesfeldt, 1975; Marshall et al., 2007; Viviant et al., 2014). However, it is pertinent to consider that this device increases the hydrodynamic resistance of the penguin, hindering its ability to perform deep dives, an incidence documented in other studies with penguins of the genus *Spheniscus* (Marshall et al., 2007; Steinfurth et al., 2008). This limitation should be taken into account when interpreting the low frequency of deep dives observed in this study.

Much of the penguin's activity occurred on or near the surface, with dominant behaviors including Prospecting and Surface Dipping. These activities appear to be exploratory strategies prior to shorter foraging dives (Ainley et al., 2010; Boersma, 1976; Steinfurth et al., 2008; Vargas et al., 2007). The structured behavioral

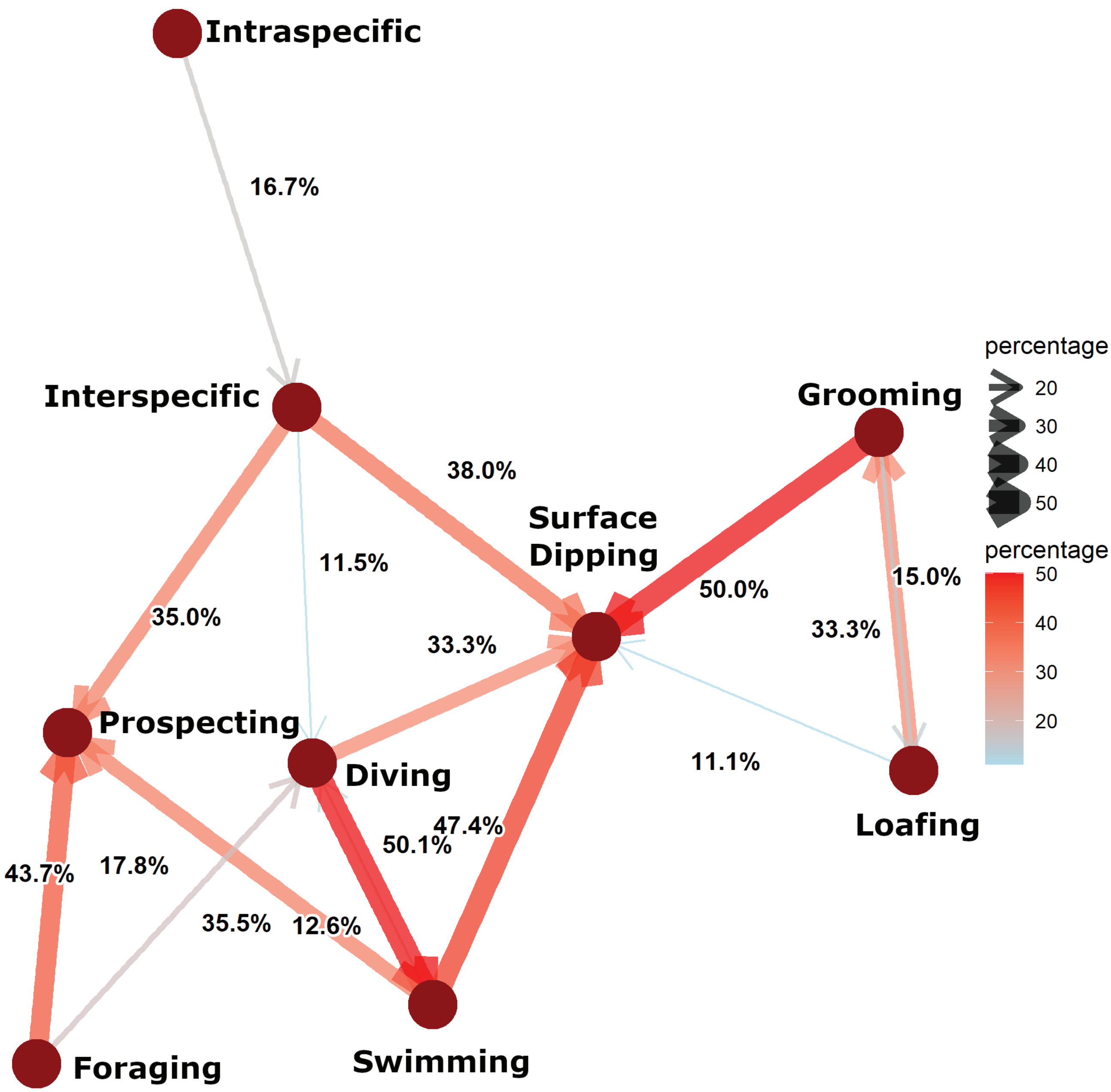

Fig. 4. Diagram illustrating the probabilities of behavioral shifts, with line thickness and color representing the likelihood of transitions between behaviors, for an adult male Galapagos Penguin *Spheniscus mendiculus* (GAPE) observed near Mariela East Islet, Galápagos.

sequence shows how animal-based video technology clarifies the organization of marine behavior, offering a context that would not be obtained with immersion data alone. The behavioral transition diagram (Fig. 4) further supports this interpretation, showing structured, nonrandom sequences—such as Swimming to Diving and Foraging to Prospecting—shaped by environmental conditions and physiological constraints. Together, these findings highlight flexible and adaptive strategies that allow GAPE to forage efficiently (see Ainley & Wilson, 2023; Boersma et al., 2013; Steinfurth et al., 2008).

A few instances of "cooperative foraging" were observed; this is a behavior involving groups of up to six penguins coordinating their movements around seaweed and rocky areas, likely intended to increase foraging efficiency by herding schools of fish (Ainley & Wilson, 2023; Gómez-Laich et al., 2018; Steinfurth, 2007; Vargas et al., 2007). While this behavior has been described in other *Spheniscus* penguins (Friard & Gamba, 2016), the present study primarily illustrates the observational value of Crittercam and does not allow conclusions regarding established group foraging behaviors, which would require multiple deployments and broader analyses (Ainley & Wilson, 2023).

A key limitation of this study is that the data were obtained from a single monitored penguin, which restricts our ability to capture the full variability in the species' behavioral repertoire. Importantly, this limitation did not arise from the equipment or methodology, but from permit conditions: managers at Galápagos National Park sought to evaluate the potential invasiveness of the technique before granting broader authorization. In addition, reproductive activity during the initial year was unusually low, and only one active nest was recorded, which limited the number of suitable individuals for deployment. Despite these constraints, the study demonstrates the feasibility, noninvasive nature, and usefulness of Crittercam deployments on *Spheniscus* penguins. It provides valuable baseline information, reveals detailed behavioral patterns, and highlights the strong potential of animal-borne video systems to advance our understanding of the species' fine-scale ecology. Moreover, this research lays a solid foundation for future studies, in which expanding the sample size will allow exploration of individual variability, group dynamics, and responses to environmental changes. Continuous improvements in device design are expected to further minimize behavioral impacts, increasing the value of video monitoring for the conservation and understanding of GAPE.

ACKNOWLEDGEMENTS

We sincerely thank our donors for their financial support of the Conservation of Galápagos Marine & Lagoon Avian Project at the Charles Darwin Foundation: Oceans Finance Company, Galapagos Conservation Trust, Truell Charitable Foundation, Leona M. and Harry B. Helmsley Charitable Trust, Lindblad–National Geographic, Penguin Fund of Japan, Mr. Seishi, Sophie Lenoir of Tunememi Conservancy, and our anonymous sponsors. We extend special thanks to our collaborators and the more than 95 assistants and volunteers who have contributed to this research since 2009, including Manuel Masaquisa and Wilson Villafuerte. We are grateful to Johny Mazón for designing the map, the Galápagos National Park Directorate for granting research permit PC-51-16, and the Charles Darwin Research Station for its ongoing support. We also sincerely appreciate the reviewers' constructive suggestions and the insightful feedback provided by editor-in-chief David Ainley and technical editor Erica Akiko Howard. This publication represents contribution number 2754 from the Charles Darwin Foundation for the Galápagos Islands.

AUTHOR CONTRIBUTIONS

Conceptualization: GM, GJU. Methodology: GM, GJU. Software: JC, WI. Validation: GJU, GM. Formal analysis: JC, WI, GJU. Research: GJU, GM, LV. Resources: GJU, GM, CS. Data curation: JC. Writing—original draft: JC, GJU, AC, LV. Writing—review & editing: all authors. Project management: GJU. Acquisition of funds: GJU, GM, CS. All authors have read and agreed to the published version of the manuscript and declare that they have no conflict of interest.

REFERENCES

Acosta Hospitaleche, C. (2005). Los pingüinos, grandes buceadores. *Museo*, *3*(19), 63–66. http://sedici.unlp.edu.ar/handle/10915/47253

Ainley, D., Russell, J., Jenouvrier, S., Woehler, E., Lyver, P. O., Fraser, W. R., & Kooyman, G. L. (2010). Antarctic penguin response to habitat change as Earth's troposphere reaches 2°C above preindustrial levels. *Ecological Monographs*, *80*(1), 49–66. https://doi.org/10.1890/08-2289.1

Ainley, D. G., & Wilson, R. P. (2023). *The aquatic world of penguins: Biology of fish-birds*. Springer. https://doi.org/10.1007/978-3-031-33990-5

Bjerknes, J. (1969). Atmospheric teleconnections from the equatorial Pacific. *Monthly Weather Review*, *97*(3), 163–172. https://doi.org/10.1175/1520-0493(1969)097<0163:ATFTEP>2.3.CO;2

Boersma, P. D. (1976). An ecological and behavioral study of the Galapagos penguin. *The Living Bird*, *15*, 43–93. https://www.biodiversitylibrary.org/page/59476356

Boersma, P. D., Steinfurth, A., Merlen, G., Jiménez-Uzcátegui, G., Vargas, F. H., & Parker, P. G. (2013). Galápagos Penguin (*Spheniscus mendiculus*). In P. Garcia Borboroglu & P. D. Boersma (Eds.), *Penguins: Natural history and conservation* (pp. 285–302). University of Washington Press.

Eibl-Eibesfeldt, I. (1975). *Las Islas Galápagos: Un arca de Noé en el Pacífico*. Alianza Editorial.

Eibl-Eibesfeldt, I. (2012). Turning points in evolution: Ethological perspectives on hominization. In M. Wolff & M. Gardener (Eds.), *The role of science for conservation* (pp. 52–86). Routledge.

Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, *7*(11), 1325–1330. https://doi.org/10.1111/2041-210X.12584

Gómez-Laich, A., Yoda, K., & Quintana, F. (2018). Insights into the foraging behavior of Magellanic penguins (*Spheniscus magellanicus*). *Waterbirds*, *41*(3), 332–336. https://doi.org/10.1675/063.041.0315

Harris, M. P. (1973). The Galápagos avifauna. *The Condor*, *75*(3), 265–278. https://doi.org/10.2307/1366166

Harris, M. P. (1974). *A field guide to the birds of Galapagos*. William Collins.

Jiménez-Uzcátegui, G. (2022). Imperiled vertebrates of the Galápagos: Pressures and solutions. In D. A. DellaSala & M. I. Goldstein (Eds.), *Imperiled: The encyclopedia of conservation* (Vol. 3, pp. 265–292). Elsevier. https://doi.org/10.1016/B978-0-12-821139-7.00140-9

Jiménez-Uzcátegui, G., & Vargas, F. H. (2019). Maximum observed ages of Galápagos Penguins. *Marine Ornithology*, *47*(2), 243–246. http://doi.org/10.5038/2074-1235.47.2.1324

Karnauskas, K. B., Jenouvrier, S., Brown, C. W., & Murtugudde, R. (2015). Strong sea surface cooling in the eastern equatorial Pacific and implications for Galápagos Penguin conservation. *Geophysical Research Letters*, *42*(15), 6432–6437. https://doi.org/10.1002/2015GL064456

Lynnes, A. S., Reid, K., Croxall, J. P., & Trathan, P. N. (2002). Conflict or co-existence? Foraging distribution and competition for prey between Adélie and chinstrap penguins. *Marine Biology*, *141*(6), 1165–1174. https://doi.org/10.1007/s00227-002-0899-1

Marshall, G. J. (1998). Crittercam: an animal-borne imaging and data logging system. *Marine Technology Society Journal*, *32*(1), 11–17.

Marshall, G., Bakhtiari, M., Shepard, M., Tweedy, J., III, Rasch, D., Abernathy, K., Joliff, B., Carrier, J. C., & Heithaus, M. R. (2007). An advanced solid-state animal-borne video and environmental data-logging device ("Crittercam") for marine research. *Marine Technology Society Journal*, *41*(2), 31–38. https://doi.org/10.4031/002533207787442240

Miller, A. K., Kappes, M. A., Trivelpiece, S. G., & Trivelpiece, W. Z. (2010). Foraging-niche separation of breeding Gentoo and Chinstrap Penguins, South Shetland Islands, Antarctica. *The Condor*, *112*(4), 683–695. https://doi.org/10.1525/cond.2010.090221

Mills, K. L. (1998). Multispecies seabird feeding flocks in the Galápagos Islands. *The Condor*, *100*(2), 277–285. https://doi.org/10.2307/1370268

RStudio Team. (2020). *RStudio: Integrated development for R* (Version 1.3.1056) [Computer software]. PBC. http://www.rstudio.com/

Ruiz, D. J., & Wolff, M. (2011). The Bolivar Channel Ecosystem of the Galapagos Marine Reserve: Energy flow structure and role of keystone groups. *Journal of Sea Research*, *66*(2), 123–134. https://doi.org/10.1016/j.seares.2011.05.006

Snell, H. M., Stone, P. A., & Snell, H. L. (1996). A summary of geographical characteristics of the Galápagos Islands. *Journal of Biogeography*, *23*(5), 619–624. https://doi.org/10.1111/j.1365-2699.1996.tb00022.x

Steinfurth, A. (2007). *Marine ecology and conservation of the Galápagos penguin,* Spheniscus mendiculus [Doctoral dissertation, University of Kiel]. MACAU [Open Access Repository of Kiel University]. https://nbn-resolving.org/urn:nbn:de:gbv:8-diss-21557

Steinfurth, A., Vargas, F. H., Wilson, R. P., Spindler, M., & Macdonald, D. W. (2008). Space use by foraging Galápagos penguins during chick rearing. *Endangered Species Research*, *4*(1–2), 105–112. https://doi.org/10.3354/esr00046

Trivelpiece, W. Z., Trivelpiece, S. G., & Volkman, N. J. (1987). Ecological segregation of Adelie, Gentoo, and Chinstrap penguins at King George Island, Antarctica. *Ecology*, *68*(2), 351–361. https://doi.org/10.2307/1939266

Vargas, F. H. (2006). *The ecology of small populations of birds in a changing climate* [Unpublished doctoral dissertation]. University of Oxford.

Vargas, F. H., Harrison, S., Rea, S., & Macdonald, D. W. (2006). Biological effects of El Niño on the Galápagos penguin. *Biological Conservation*, *127*(1), 107–114. https://doi.org/10.1016/j.biocon.2005.08.001

Vargas, F. H., Lacy, R. C., Johnson, P. J., Steinfurth, A., Crawford, R. J. M., Boersma, P. D., & Macdonald, D. W. (2007). Modelling the effect of El Niño on the persistence of small populations: The Galápagos penguin as a case study. *Biological Conservation*, *137*(1), 138–148. https://doi.org/10.1016/j.biocon.2007.02.005

Viviant, M., Monestiez, P., & Guinet, C. (2014). Can we predict foraging success in a marine predator from dive patterns only? Validation with prey capture attempt data. *PLOS One*, *9*(3), Article e88503. https://doi.org/10.1371/journal.pone.0088503