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OPTIMIZING THE USE OF GPS DEVICES TO ESTIMATE HOME RANGE AND FORAGING AREAS IN SEABIRDS: THE IMPERIAL SHAG (*Leucocarbo atriceps*) AS A CASE STUDY

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ABSTRACT: Although GPS devices are widely used to delineate animal use areas, the sample size required to yield statistically robust estimates while minimizing animal welfare concerns is seldom assessed. In this study, we assessed how sample size (i.e., the number of individuals equipped with GPS devices) affects the accuracy of estimating both the total area of active use and the core foraging area of the Imperial Shag (*Leucocarbo atriceps*). We analyzed data from 140 breeding adults tracked over seven breeding seasons at Punta León (Chubut, Argentina). For each season, estimates of active use and core foraging areas were derived by progressively increasing the sample size from one to 20 individuals. Additionally, given sexual differences in foraging behavior, use and core foraging areas were estimated separately for females and males by progressively increasing sample sizes from one to 10 individuals per sex and year. On average, a minimum of 13 individuals was required to achieve < 5% increments in estimated area sizes. Tagging between 10 and 12 males and females was sufficient to estimate use and core foraging areas with an error below 5%. This study provides a straightforward approach to determine the minimum number of birds to tag, which can be adapted to other species with comparable movement patterns.

KEYWORDS: *birds, Global Positioning System, GPS, home range area, IBAs, sample size*

Animals perform a wide diversity of movements, both to acquire resources (i.e., food, mate, and shelter) and to escape from predators (Swingland & Greenwood 1983). These movements influence the configuration of population distribution patterns, the ecological role of species, and the spread of diseases, among other ecosystem characteristics (Nathan 2008, Kays et al. 2015). In this way, the analysis of animal movement has been central to studies in ecology, behavior, evolutionary biology, and environmental ecology (Nathan et al. 2022).

Among the most widely used electronic devices are Global Positioning Systems (GPS), which record positional information (latitude – longitude) at time intervals that may vary from seconds to days (Quintana et al. 2024). The information collected by these loggers allows, for example, the analyses of the trajectories of instrumented individuals and the determination of population use areas (Langley et al. 2021). In the field of conservation, positional data obtained through the use of GPS devices contribute to the design of management plans. These data allow the evaluation of the degree of overlap between the areas and routes used by individuals and various anthropogenic activities, such as commercial fishing (Copello & Quintana 2009, Yorio et al. 2010, Copello et al. 2014, 2016), the dis-

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tribution and abundance of plastic pollutants (Blanco et al. 2022, Clark et al. 2023), and agriculture (Lenz et al. 2015), among others. In turn, information on movement and space use obtained from GPS devices is fundamental for the identification and delineation of Important Bird Areas (IBAs) and Key Biodiversity Areas (KBAs ; Eken et al. 2004, Beal et al. 2021).

In the particular case of birds, information obtained from the use of GPS devices plays a fundamental role in the program of BirdLife International to determine IBAs (Lascelles et al. 2016). This program aims to define key areas for conservation at global and regional levels (Thiollay 2002, Donald et al. 2019). Although IBAs were originally developed and applied in terrestrial and freshwater environments (Fishpool & Evans 2001), their application in marine environments has become widely practiced in recent decades (BirdLife International 2009). For their identification, design, and monitoring, the positional information in time and space of seabirds obtained through the use of GPS devices is fundamental (Lascelles et al. 2016, Beal et al. 2021).

A recent review of the use of biologgers in South American seabirds indicates that the use of GPS devices has encompassed 28 species belonging to nine families and five orders, and that almost all of the consulted publications (more than 250) contain information derived from positioning devices (Quintana et al. 2024). Despite their widespread use and the relevance of obtaining information that allows, for example, the proper delineation of IBAs and KBAs, studies analyzing the minimum number of animals to be tagged for the correct identification of the use areas of a given population are virtually nonexistent (Soanes et al. 2013, 2014, Lascelles et al. 2016, Beal et al. 2021, Shimada et al. 2021, He et al. 2023). In most cases, the number of equipped animals is mainly subject to the availability of time and funds for the acquisition and deployment of instruments. However, an insufficient sample size may compromise the robustness of population inference (Lindberg & Walker 2007, Hebblewhite & Haydon 2010, Soanes et al. 2013), whereas an excessive sample size may have ethical implications related to animal welfare (Bodey et al. 2018, Quintana et al. 2024, Arrondo & Pérez-García 2025). Thus, analyzing the optimal use of technology becomes important for the efficient allocation of funds and time invested in data collection and analysis, and for considering the ethical aspects related to animal welfare by avoiding excessive manipulation of individuals (Soanes et al. 2013, Williams et al. 2020, Quintana et al. 2024).

The goal of this study was to evaluate the effect of sample size (i.e., number of individuals tagged with GPS devices) on the precision of estimating the use of marine areas. As a case study, we used the Imperial Shag (*Leucocarbo atriceps*), a diving seabird with benthic habits (Malacalza et al. 1994, Quintana et al. 2011, Gómez Laich et al. 2012). We examined interannual variability in the minimum sample size (i.e., birds to be instrumented) required to determine the size of: a) active use marine areas (transit and feeding); and b) core foraging areas (where shags dive in search of prey). We carried out these estimations both for the population as a whole and separately for each sex, given the sexual dimorphism in size (Svagelj & Quintana 2007), as well as the differences in behavior and space use reported in previous studies (Quintana et al. 2011, Gómez Laich et al. 2012).

METHODS

Study species

The Imperial Shag is a diving seabird whose distribution along the Argentine coast extends from Punta León (43°S) in Chubut Province to the Beagle Channel (55°S) in Tierra del Fuego Province (Frere et al. 2005, Quintana et al. 2022). During the breeding season, these birds behave as central-place foragers (Orians & Pearson 1979), making regular feeding trips to the sea and returning to the colony to incubate the clutch and protect and feed the chicks (Quintana et al. 2011, 2022). Males and females exhibit sexual size dimorphism (Svagelj & Quintana 2007) and show spatial segregation in relation to foraging areas (Quintana et al. 2011) and differences in feeding and diving behavior (Gómez Laich et al. 2012).

Database and study site

For this study we used a database of at-sea positions obtained from the deployment of GPS loggers during the foraging trips of breeding adult Imperial shags from the Punta León colony (43°04’S, 64°29’W), Chubut, Argentina (Fig. 1). Thus, we used a long-term dataset that includes information obtained from the instrumentation of a total of 140 individuals (20 individuals per year, 10 of each sex) over seven breeding seasons (2008–10, 2013, 2015–17). All instrumented shags were in the early chick-rearing period (four to 15 days old). To attach the devices, we removed the animals from their nests using a hook specially designed for this task and determined the sex of each individual from its vocalizations (males produce a ‘*honk*’ and females a ‘*hiss*’; Malacalza & Hall 1988, Svagelj & Quintana 2007). We placed the GPS devices on the lower back using Tesa tape model 4621 (Wilson et al. 1997), and captured and instrumented each bird in approximately five minutes. In no case did the weight of the device exceed 3% of the animal's body mass (Kenward 2001). During the seven years of study we used three types of loggers: (1) GPS (GPSlog, Earth and Ocean Technologies, Kiel, Germany, 95 × 48 × 24 mm and 65 g); (2) MiniGPS (Earth and Ocean Technologies, Kiel, Germany, 45 × 30 × 20 mm and 30.5 g); and (3) AXY-Trek (TechnoSmart, Rome, Italy, 40 × 20 × 8 mm and 25 g). In total, we instrumented 36 individuals with GPS devices (13 females, 23 males), 66 with MiniGPS devices (38 females, 28 males), and 38 with AXY-Treks (19 females, 19 males). In all cases, we programmed the instruments to record latitude and longitude at a frequency of 1 Hz (one datum per second), and they remained on the birds for a single feeding trip at sea. Upon return from the trip, we recaptured the birds in the same way described above, and the instruments and Tesa tape were carefully removed. We carried out this procedure in less than three minutes.

Data analysis

Classification of positions

Following the methodology proposed by Quintana et al. (2011), we classified each of the positions recorded during feeding trips at sea according to the following behaviors: flight, floating, or diving. To do this, we used algorithms obtained from the observation of the frequency distribution of the horizontal travel speed associated with each position and the duration of interruptions in the GPS signals generated by the lack of transmission from the device when animals are underwater (Quintana et al. 2011). We classified as 'flight' all positions with speeds greater than 3 m/s, as 'diving' all positions with speeds equal to or less than 3 m/s and an interruption greater than or equal to 8 s, and as 'floating' positions with speeds equal to or less than 3 m/s and an interruption shorter than 8 s (Quintana et al. 2011).

Determination and calculation of marine areas of active use and core foraging areas

To calculate marine areas of active use and core foraging areas, we first constructed a grid with 1 km² cells in the marine zone surrounding the colony (Page et al. 2006). This grid was built using the POSGAR belt 3 projection (Alberdi & Erba 2022), which resulted in a total of 6768 cells. Thus, for each breeding season we calculated the size of the marine use area by counting the total number of cells used by the animals considering all recorded positions (regardless of the behavior associated with each of them). For the determination of the core foraging area, in contrast, we counted the number of cells where animals performed dives (that is, only those positions classified as diving were used; Fig. 2).

For each season, we calculated the size of the active use and core foraging areas for an increasing sample of animals (from one to 20 individuals, representing all birds equipped per season). We selected the individuals included in each sample 20 times at random and with replacement. That is, for *n* = 1, we randomly

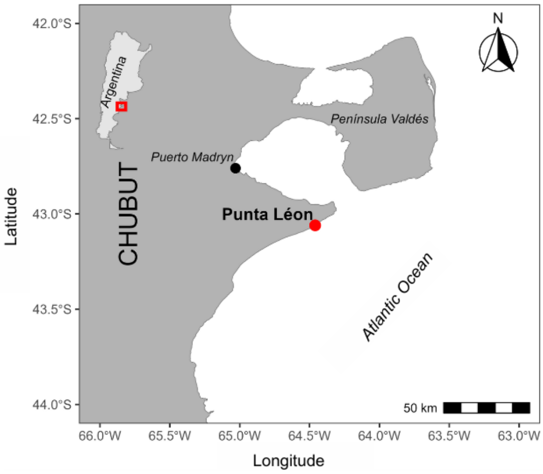

Figure 1. Location of the Imperial Shag (*Leucocarbo atriceps*) colony at Punta León on the coast of Chubut Province, Argentina.

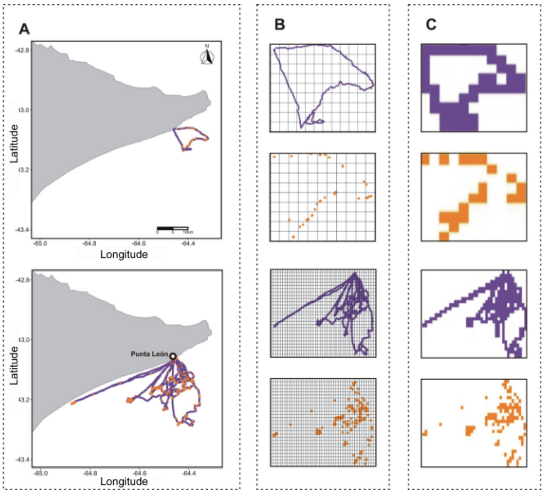

Figure 2. Determination of the marine areas of active use and core foraging of Imperial shags (*Leucocarbo atriceps*) equipped with GPS at the Punta León colony, Chubut, Argentina, during the chick-rearing period. A) Foraging trajectories of a single individual (upper panel) and of 20 individuals (lower panel) during one breeding season, B) overlay of the trajectories on a grid with 1 km² cells, and C) cells used during foraging trips. Purple points represent all recorded positions, while orange points show only those classified as dives.

selected with replacement one individual on 20 occasions and calculated the areas for each individual (20 active use areas and 20 core foraging areas in total). For n = 2, we randomly selected with replacement two individuals and calculated the areas for the 20 pairs of individuals, and so on. We used the same process to determine the minimum number of females and males to be tagged to establish both the size of the marine use area and the core foraging area for each sex. In this case, we calculated the areas for an increasing sample of individuals ranging from one to 10 according to the number of birds of each sex equipped in each season. We selected the individuals included in each sample 10 times at random and with replacement. Thus, for each sex we proceeded as follows: for n = 1, we randomly selected with replacement one individual 10 times and calculated the areas for each individual (10 active use areas and 10 core foraging areas in total). For n = 2, we randomly selected with replacement two individuals and calculated the areas for the 10 pairs of individuals, and so on. In this way, we obtained, for both females and males, 10 estimates of the active use area and 10 estimates of the core foraging area for each sample size (from one to 10).

Once the areas were calculated as a function of the increasing number of sampled individuals, we constructed accumulation curves of the size of the marine use area and core foraging area in relation to the number of individuals included in the sample, for the entire breeding population of the study site, composed of 13,200 individuals (6600 breeding pairs; Quintana et al. 2022). We fitted these curves using the Michaelis–Menten model with the function *drm* from the library *drc* (Knezevic et al. 2007) in the open-access software R version 4.2.3 (R Core Team 2022). The choice of this model was based on the fact that in several species of seabirds during the breeding season, the relationship between the number of individuals considered and the size of the active use and/or core foraging areas tends to stabilize as sample size increases, reaching an asymptote that represents the maximum area used (Soanes et al. 2013). This pattern reflects the spatial, energetic, and temporal constraints faced by central-place foragers (Orians & Pearson 1979). In the case of the Imperial Shag, these limitations are related both to morphological and physiological factors, mainly associated with the trade-offs involved in being both a diving and flying bird (Bishop & Butler 1995, Watanabe et al. 2011, Wilson et al. 2012, Gómez-Laich et al. 2013), and to aspects of its reproductive biology linked to biparental care and the need to return periodically to the colony to attend and feed the chicks (Schreiber & Burger 2001, Quintana et al. 2011, Harris et al. 2013).

The Michaelis–Menten model has two parameters: 1) V_{max}, which corresponds to the value of the asymptote (that is, in this case, the size of the area that remains constant despite an increase in sample size), which from now on will be referred to as A_{max}; and 2) K_m, which in this study corresponds to the number of animals to tag for which the active use or core foraging area (depending on the case) is half the value of the area represented by the asymptote, which from now on will be referred to as T_m (Johnson & Goody 2011; Fig. 3). Because T_m constitutes a purely arithmetic parameter derived from the model equation and does not have practical significance for the objectives of this study, the results mainly discuss aspects associated with the parameter A_{max}.

Statistical analyses

Determination of the minimum sample size

To analyze interannual variation in sample size (i.e., minimum number of individuals to be tagged) to estimate the size of the active marine use and core foraging areas of the entire population and for each sex, we determined the relevance of including the explanatory variable year in the Michaelis–Menten models and its effect on the parameters A_{max} and T_m. To analyze the relationship between sample size and the size of active use and core foraging areas, we compared the following four models: 1) a model without including the variable year/sex as an explanatory variable, 2) a model including the effect of the variable year/sex on the parameters A_{max} and T_m, 3) a model including the effect of the variable year/sex only on the parameter A_{max}, and 4) a model including the effect of the variable year/sex only on the parameter Tm. The four models were constructed using the function *nls* from the library *nlme* (Pinheiro et al. 2007). We ranked the models according to the minimization of the corrected AIC (AICc), subsequently calculated the ΔAICc between them, and selected the model with the lowest ΔAICc (Anderson & Burnham 2002). In those cases in which several models had a ΔAICc ≤ 4, we selected the most parsimonious model (i.e., the one that included fewer parameters; Lehikoinen et al. 2021). To calculate both the AICc and the AICc weight (AICcw) of each model, as well as the ΔAICc between models, we used the function *aictab* from the library *AICcmodavg* (Mazerolle 2020).

In all cases, we verified the assumptions of normality and homoscedasticity of the best model. If

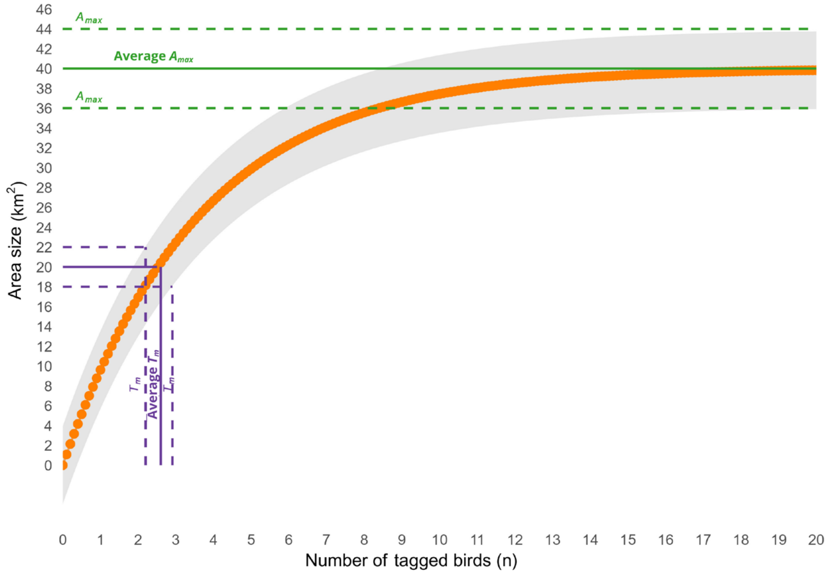

Figure 3. Illustrative example of the Michaelis–Menten model with its two parameters, A_{max} and T_m. In orange, the relationship between area size and sample size (i.e., number of tagged birds) is shown, while the gray shading indicates the confidence interval of the curve. The parameters obtained from the model ($T_m = 2.5$ and $A_{max} = 40$) and the lower ($T_m = 3$ and $A_{max} = 36$) and upper ($T_m = 2$ and $A_{max} = 44$) values of each parameter obtained from the confidence intervals are also indicated.

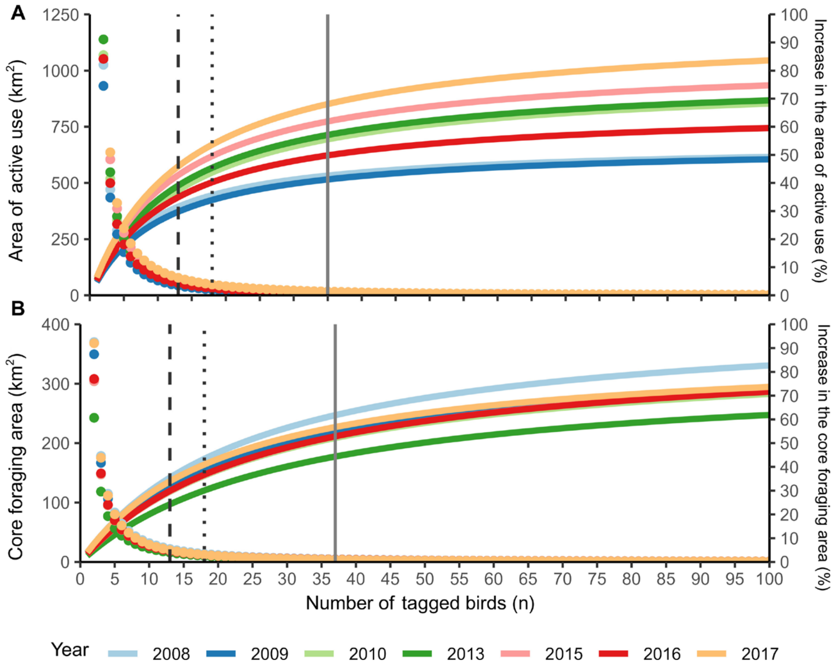

Figure 4. Sizes of the areas of active use (A) and core foraging (B) (solid lines) with their respective percentages of increase (dotted lines), in relation to sample size for the Imperial Shag (*Leucocarbo atriceps*), for the seven study years. In both graphs, the vertical dashed, dotted, and solid lines indicate the average minimum number of animals to instrument such that adding one more individual to the sample increases the area by less than 5%, 3%, and 1%, respectively.

heteroscedasticity were detected, we modeled the variance using the variance structure *varExp*. In those cases in which the best-fitting model included the variable year, we performed contrast tests of the parameter A_{max}, T_m, or both (as appropriate) among all years through post hoc multiple comparison tests using the function *paircomp* from the library *aomisc* (Onofri 2020) with the Holm correction (Aickin &

Gensler 1996). We estimated the increase in the size of the active use area and the core foraging area as a function of the number of shags included in the sample using the best-fitting model for each case. Subsequently, in order to evaluate with different levels of precision the size of the use and feeding areas by year/sex, we calculated the minimum sample size and its range from which adding one more individual to the sample resulted in an increase in area (active use or core foraging) of less than 5, 3, and 1%, with the 1% criterion representing the highest precision and the 5% criterion the lowest. To obtain the minimum and maximum values, that is, the range of the minimum sample size, we first calculated the confidence interval of the parameters of the best model for the active use marine area. Analogously, we obtained the confidence interval for the core foraging area. In both cases, the intervals were obtained using the function *confint* (Ripley et al. 2013). With the minimum and maximum values of each parameter we constructed the lower and upper curves of the relationship between area size and sample size. We used the lower curve to estimate the minimum value of the range of sample size from which the increase in area was less than 5, 3, and 1%, while we used the upper curve to estimate the maximum value (Fig. 3). We based the evaluation of differences in the sample size required to estimate the size of the marine active use area and core foraging area of individuals between years and between sexes within each year on the overlap of the ranges of predicted values for each case. We conducted all analyses with the open-access software R version 4.2.3 (R Core

Table 1. Michaelis–Menten models for the relationship between active use and core foraging area sizes as a function of sample size for the Imperial Shag (*Leucocarbo atriceps*). In each case, the best model is shown in bold. The table presents: the number of parameters (k), the difference in AICc between each model and the best-fitting model (ΔAICc), the AIC weights (AICcw), and the cumulative sum of AICcw weights (Cum.wt).

Response variable	Model	k	AICc	ΔAICc	AICcw	Cum.wt
Active use area	**A_{max}~Year, T_m~ Year**	**15**	**30855**	**0**	**1**	**1**
	A_{max}~ Year, T_m~1	9	30871	16.2	0	1
	A_{max}~1, T_m~ Year	9	31029	174.4	0	1
	A_{max}~1, T_m~1	3	32761	1906.3	0	1
Core foraging area	A_{max}~ Year, T_m~ Year	15	23414	0	0.5	0.5
	A_{max}~1, T_m~ Year	**9**	**23415**	**0.6**	**0.4**	**0.9**
	A_{max}~ Year , T_m~1	9	23418	4.5	0.1	1
	A_{max}~1, T_m~1	3	24655	1241.3	0	1

Table 2. Year-specific parameter estimates of the Michaelis–Menten model used to predict the sizes of active use and core foraging marine areas as a function of sample size for the Imperial Shag (*Leucocarbo atriceps*) at the Punta León (Chubut, Argentina) colony. Confidence intervals are indicated [Min–Max]. Significant multiple comparison tests for the parameter A_{max} are indicated with an asterisk (*), whereas significant differences among years for the parameter T_m are indicated with a black triangle ($^{\Delta}$).
Active use area: * (2008 vs 2010, 2013, 2015, 2016, 2017); ** (2009 vs 2010, 2013, 2015, 2016, 2017); *** (2016 vs 2010, 2013, 2015, 2017); **** (2017 vs 2010, 2013, 2015); $^{\Delta}$ (2008 vs 2010, 2013, 2015, 2017); $^{\Delta\Delta}$ (2009 vs 2010, 2017).
Core foraging area: $^{\Delta}$ (2008 vs 2009, 2010, 2013, 2015, 2016, 2017); $^{\Delta\Delta}$ (2009 vs 2010, 2013, 2015, 2016, 2017); $^{\Delta\Delta\Delta}$ (2013 vs 2010, 2015, 2016, 2017); $^{\Delta\Delta\Delta\Delta}$ (2017 vs 2010, 2015, 2016).

Year	**A_{max}**		**T_m**	
	Active use area (km^2)	Core foraging Area (km^2)	Active use area (*n* of animals)	Core foraging area (*n* of animals)
2008	674 [640-707] *	399 [361-437]	9 [8-10] $^{\Delta}$	24 [20-27] $^{\Delta}$
2009	672 [625-719] **	323 [293-352]	10 [9-12] $^{\Delta\Delta}$	19 [16-22] $^{\Delta\Delta}$
2010	1010 [925-1095]	364 [318-411]	15 [13-17]	27 [22-32]
2013	1000 [920-1079]	311 [267-355]	14 [12-16]	29 [23-35] $^{\Delta\Delta\Delta}$
2015	1066 [999-1133]	356 [311-401]	13 [11-14]	26 [21-31]
2016	819 [769-869] ***	359 [311-407]	11 [10-13]	26 [21-31]
2017	1169 [1072-1266] ****	347 [313-382]	13 [11-16]	20 [17-24] $^{\Delta\Delta\Delta\Delta}$
Mean	916 [672-1169]	351 [311-399]	12 [9-15]	24 [19-29]

Team 2022) considering a significance level of 0.05.

RESULTS

Determination of the minimum sample size for the population

For all study years, the size of the active use area increased as the number of birds included in the sample increased until reaching an asymptote, and the relationship between both variables differed among years (Fig. 4A, Tables 1 & 2). The size of the active use area of the breeding population averaged 916 km² and ranged between 672 and 1169 km² (Table 2). The main differences in the sizes of the use areas corresponded to the 2008, 2009, and 2017 seasons. During the 2008 and 2009 seasons, the estimated areas used by breeding adults were smaller than in the other seasons (*post hoc* contrasts for parameter A_{max} between 2008 and 2009 vs. 2010, 2013, 2015, 2016, and 2017; $p < 0.001$, Table 2), whereas during 2017 it was larger than in the other seasons (*post hoc* contrasts for parameter A_{max} between 2017 and 2008, 2009, 2010, 2013, 2015, and 2016; $p < 0.05$, Table 2).

The model that best represented (i.e., best fit and parsimony) the relationship between core foraging area size and sample size included the explanatory variable year affecting parameter T_m but not A_{max}. Thus, the size of the core foraging area of the breeding population did not differ among years and averaged 351 km² (Fig. 4B, Tables 1 & 2).

The average minimum number of animals to be tagged to estimate the size of the use area was 13 (range = 11–16), 18 (range = 15–22), and 35 (range = 27–42) for increases in area smaller than 5, 3, and 1%, respectively (Fig. 5A). In 2008 and 2009, the number of animals to tag was, in all cases, lower than in the other years, whereas in 2017 it was higher (Fig. 5A).

The size of the core foraging area of the breeding population (mean: 351 km²; range: 311–399 km²) did not differ among seasons (Table 2). In general terms, the average minimum number of shags to be tagged to estimate the core foraging area of the entire population showed less variation among years compared with the sample size required for the use area (Fig. 5B). The average minimum number of animals to be tagged to determine the core foraging area was 13 (range = 12–14), 19 (range = 17–19), and 39 (range = 37–40) with precisions smaller than 5, 3, and 1%, respectively (Fig. 5B). The main differences corresponded to the 2013 season, in which the sample size from which the increase in area was smaller than 5% was lower than in the other seasons (Fig. 5B). Likewise, the number of animals to be tagged from which the increase in core foraging area was smaller than 3% was lower in 2013 compared with 2008, 2009, and 2017, whereas the sample size for precisions smaller than 1% was similar across the seven study years, showing differences only between 2013 and 2008 (Fig. 5B).

Determination of the minimum sample size for each sex

In all seasons, the size of the active use and core foraging areas for both females and males increased with increasing sample size until reaching an asymptotic value (Fig. 6). The effect of sex on the relationship between use area size and sample size varied among seasons (Table 3). Whereas in the 2008, 2010, 2013, and 2015 seasons no differences between sexes were observed (Fig. 6, Table 4), in 2009 and 2016 the use areas were larger for females and in 2017 for males (Fig. 6, Tables 3 & 4). During the study period, females and males showed the same average active use area size (parameters A_{max}), on the order of 600 km² (Fig. 6, Table 3). In general terms, the average number of animals to be tagged from which the increase in use area was smaller than 5, 3, and 1% was similar between sexes (Fig. 7A). Thus, the average minimum number of females to be tagged was 10 (range = 9–11), 14 (range = 12–15), and 25 (range = 22–28), and for males 10 (range = 8–12), 13 (range = 11–15), and 25 (range = 20–28), for area increases of 5, 3, and 1%, respectively (Fig. 7A). The largest difference between sexes in the number of birds tagged to estimate the use area occurred in 2009. In that season, more females than males were required to estimate the size of the use area (Fig. 7A).

The effect of sex on the relationship between core foraging area size and sample size also varied among seasons (Table 5). Whereas in the 2008, 2010, 2015, and 2016 seasons females and males showed feeding areas of similar size, during 2009, 2013, and 2017 females foraged over larger areas (Fig. 6, Tables 5 & 6). In general terms, during the study period females and males fed in areas of similar average size (parameters A_{max}), covering approximately 200–230 km² (Fig. 6, Table 6). Broadly speaking, the average number of animals to be tagged from which the increase in feeding area was smaller than 5, 3, and 1% was similar between sexes (Fig. 7B). Thus, the average minimum number of females to be tagged was 12 (range = 11–13), 17 (range = 14–19), and 32 (range = 26–36), and for males 12 (range = 10–14), 16 (range = 14–19), and 32 (range = 27–35), for area increases of 5, 3, and 1%, respectively (Fig. 7B).

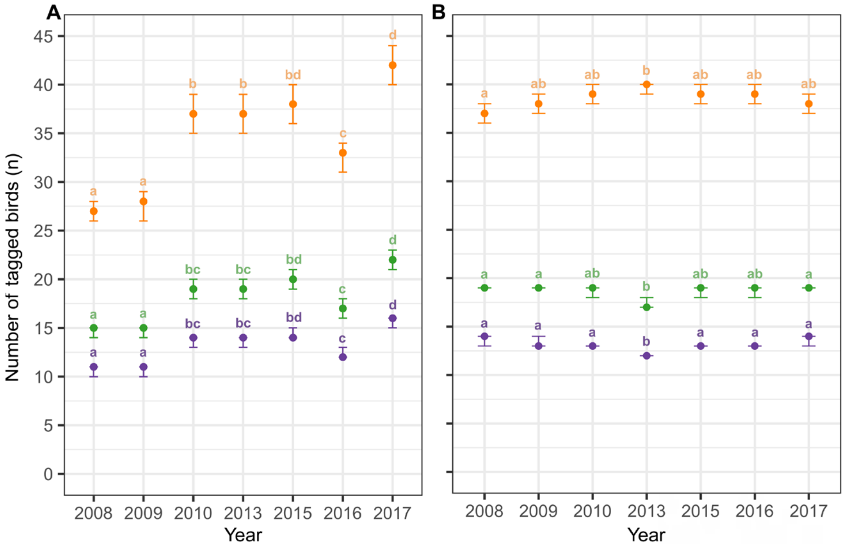

Figure 5. Number of Imperial shags (*Leucocarbo atriceps*) from the Punta León (Chubut, Argentina) colony tagged to estimate the size of the marine area of active use (A) and core foraging (B). Mean values and their ranges are presented for the sample size required so that the inclusion of one additional individual increases the estimated area by less than 1% (orange), 3% (green), and 5% (purple). Identical letters indicate no differences among years.

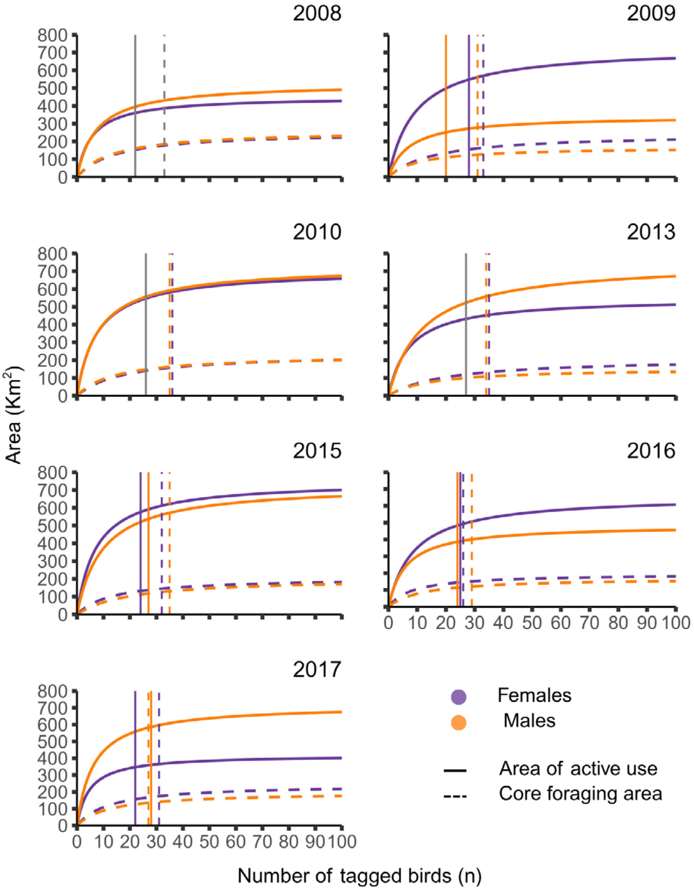

Figure 6. Sizes of the areas of active use (solid lines) and core foraging (dotted lines) of female and male Imperial shags (*Leucocarbo atriceps*) as a function of sample size, for the seven study years. Vertical lines (purple for females, orange for males, and gray if there were no differences between sexes) indicate the average minimum number of animals that must be tagged, from which point the inclusion of a new animal results in an increase of less than 1% in the size of the area of use (solid lines) or foraging (dotted lines).

Table 3. Michaelis–Menten models for the relationship between active use area size and sample size for female and male Imperial shags (*Leucocarbo atriceps*) across the seven study years. In each case, the best model is shown in bold. The table presents: the number of parameters (k), the difference in AICc between each model and the best-fitting model (ΔAICc), the AIC weights (AICcw), and the cumulative sum of AICcw weights (Cum.wt).

Year	Model	k	AICc	ΔAICc	AICcw	Cum.wt
2008	**A_{max}~1, T_m~1**	**3**	**2090**	**0**	**0.5**	**0.5**
	A_{max}~Sex, T_m~1	4	2092	1.6	0.2	0.7
	A_{max}~1, T_m~Sex	4	2092	1.8	0.2	0.9
	A_{max}~Sex, T_m~Sex	5	2093	2.9	0.1	1
2009	**A_{max}~Sex, T_m~1**	**4**	**2085**	**0**	**0.7**	**0.7**
	A_{max}~Sex, T_m~Sex	5	2087	1.6	0.3	1
	A_{max}~1, T_m~Sex	4	2094	8.5	0	1
	A_{max}~1, T_m~1	3	2308	223.2	0	1
2010	**A_{max}~1, T_m~1**	**3**	**2214**	**0**	**0.6**	**0.6**
	A_{max}~Sex, T_m~1	4	2216	2.1	0.2	0.7
	A_{max}~1, T_m~Sex	4	2216	2.1	0.2	0.9
	A_{max}~Sex, T_m~Sex	5	2218	4.2	0.1	1
2013	A_{max}~Sex, T_m~Sex	5	2051	0	0.4	0.4
	A_{max}~Sex, T_m~1	4	2052	1	0.3	0.7
	A_{max}~1, T_m~Sex	4	2053	2	0.2	0.9
	A_{max}~1, T_m~1	**3**	**2053**	**2.2**	**0.1**	**1**
2015	**A_{max}~1, T_m~Sex**	**4**	**2121**	**0**	**0.5**	**0.5**
	A_{max}~Sex, T_m~1	4	2123	1.1	0.3	0.8
	A_{max}~Sex, T_m~Sex	5	2124	2.1	0.2	1
	A_{max}~1, T_m~1	3	2174	52.3	0	1
2016	A_{max}~Sex, T_m~Sex	5	2053	0	0.5	0.5
	A_{max}~Sex, T_m~1	**4**	**2053**	**0.2**	**0.4**	**0.9**
	A_{max}~1, T_m~Sex	4	2056	3.5	0.1	1
	A_{max}~1, T_m~1	3	2074	20.8	0	1
2017	**A_{max}~Sex, T_m~1**	**4**	**2173**	**0**	**0.6**	**0.6**
	A_{max}~Sex, T_m~Sex	5	2174	1	0.4	1
	A_{max}~1, T_m~Sex	4	2184	11.8	0	1
	A_{max}~1, T_m~1	3	2309	136.5	0	1

DISCUSSION

In this study, the long-term analysis (i.e., seven years) of interannual and sex-related variability in the active use and core foraging areas of the Imperial Shag allowed us to estimate the minimum number of individuals to be tagged to determine the sizes of these areas with three different levels of precision. To achieve this, we used a simple procedure that could potentially be applied to other species with similar ecological characteristics.

The sizes of core foraging areas were more consistent among seasons than that of active use areas, which resulted in lower interannual variability in the sample sizes required to estimate them. This consistency was even more evident when comparing between sexes. Long-term spatial stability in the use of foraging areas by shags from Punta León has previously been reported by Quintana et al. (2022) in a study spanning more than 10 years, and has also been documented in other seabird species when food patches remain relatively stable in time and space (Weimerskirch 2007, Rebstock

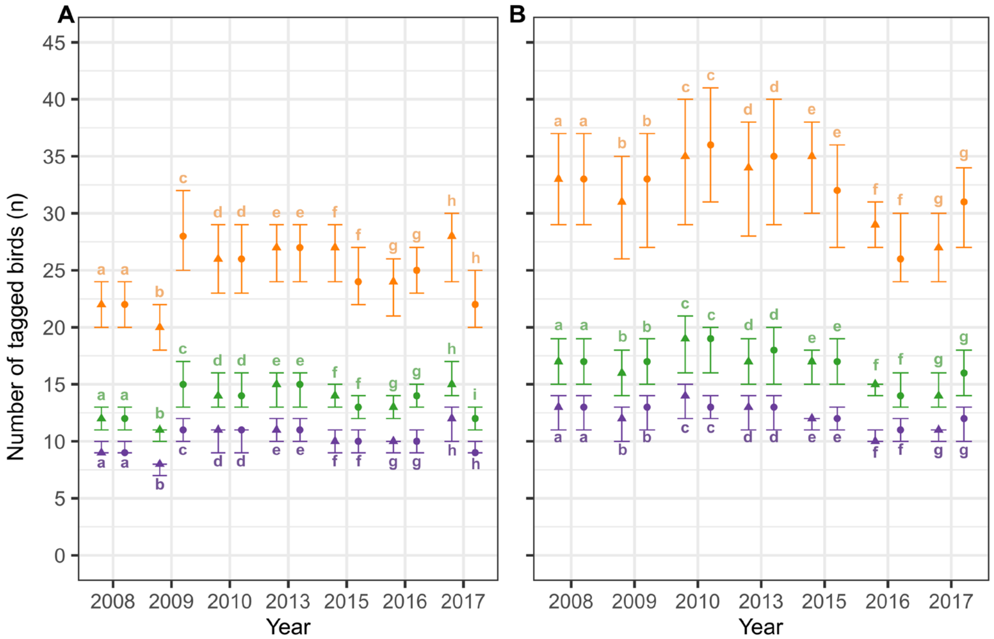

Figure 7. Numbers of female (circles) and male (triangles) Imperial shags (*Leucocarbo atriceps*) from the Punta León (Chubut, Argentina) colony tagged to estimate the size of the marine area of use (A) and foraging (B). Mean values and their corresponding ranges are presented for the sample size required so that the inclusion of one additional individual increases the estimated area by less than 1% (orange), 3% (green), and 5% (purple). Identical letters within each year for each percentage indicate no differences between sexes.

Table 4. Estimated parameters of the Michaelis–Menten model that showed the best fit for each year to predict marine area use as a function of sample size for female and male Imperial shags (*Leucocarbo atriceps*) at the Punta León (Chubut, Argentina) colony. The confidence interval [Min–Max] is indicated. Significant comparisons between sexes for the parameters A_{max} and T_m are shown in bold.

Year	A_{max}		T_m	
	Female active use area (km^2)	Male active use area (km^2)	Female active use area (*n* of animals)	Male active use area (*n* of animals)
2008	452 [351-552]	526 [425-627]	6 [3-8]	7 [5-10]
2009	**731 [547-914]**	**343 [270-417]**	9 [5-13]	7 [4-10]
2010	709 [567-850]	728 [534-922]	8 [5- 10]	8 [4-12]
2013	550 [454-645]	750 [545-956]	7 [5-10]	12 [7-17]
2015	752 [638-865]	729 [535-922]	**7 [5-9]**	**10 [5-14]**
2016	**661 [526-797]**	**484 [405-564]**	9 [6-12]	6 [4-8]
2017	**420 [338-503]**	**717 [601- 834]**	5 [3-7]	6 [4-8]
Mean	610 [420-752]	611 [343-750]	7 [5-9]	8 [6-12]

et al. 2022, Regan et al. 2024). In our case, this stability is mainly related to the benthic feeding habits and the type of prey consumed by the Imperial Shag during the early chick-rearing stage (Harris et al. 2014, Quintana et al. 2022). During this period, adults obtain both their own food and that supplied to chicks primarily by capturing benthic prey such as notothenids (*Riberoclinus* sp.) and Raneya (*Raneya brasiliensis*; Malacalza et al. 1994, Ibarra et al. 2022). In general, benthic prey have a more restricted movement range than pelagic prey, making them a food source with greater spatiotemporal predictability (Elliott et al. 2009). In this context, it is reasonable to expect that the minimum number of Imperial shags to be tagged to determine foraging areas would be more consistent among seasons than the number required to determine active use areas. The latter are subject to intrinsic conditions of individuals such as flight capacity and/or strategies required

Table 5. Michaelis–Menten models for the relationship between core foraging area size and sample size for female and male Imperial shags (*Leucocarbo atriceps*) for the seven study years. In each case, the best model is shown in bold. The table shows: the number of parameters (k), the difference in AICc between each model and the best-fitting model (ΔAICc), the AIC weights (AICcw), and the cumulative sum of the AICcw weights (Cum.wt).

Year	Model	k	AICc	ΔAICc	AICcw	Cum.wt
2008	$A_{max} \sim \mathrm{Sex}, T_m \sim 1$	4	1623	0	0.4	0.4
	$A_{max} \sim 1, T_m \sim \mathrm{Sex}$	4	1623	0	0.4	0.7
	$A_{max} \sim 1, T_m \sim 1$	**3**	**1624**	**1.5**	**0.2**	**0.9**
	$A_{max} \sim \mathrm{Sex}, T_m \sim \mathrm{Sex}$	5	1625	2.1	0.1	1
2009	**$A_{max} \sim \mathrm{Sex}, T_m \sim 1$**	**4**	**1583**	**0**	**0.5**	**0.5**
	$A_{max} \sim \mathrm{Sex}, T_m \sim \mathrm{Sex}$	5	1584	0.8	0.3	0.8
	$A_{max} \sim 1, T_m \sim \mathrm{Sex}$	4	1584	1.1	0.3	1
	$A_{max} \sim 1, T_m \sim 1$	3	1593	10.3	0	1
2010	**$A_{max} \sim 1, T_m \sim \mathrm{Sex}$**	**4**	**1559**	**0**	**0.5**	**0.5**
	$A_{max} \sim \mathrm{Sex}, T_m \sim 1$	4	1559	0.3	0.4	0.8
	$A_{max} \sim \mathrm{Sex}, T_m \sim \mathrm{Sex}$	5	1561	2.1	0.2	1
	$A_{max} \sim 1, T_m \sim 1$	3	1573	14	0	1
2013	**$A_{max} \sim \mathrm{Sex}, T_m \sim 1$**	**4**	**1458**	**0**	**0.4**	**0.4**
	$A_{max} \sim 1, T_m \sim \mathrm{Sex}$	4	1458	0.4	0.3	0.8
	$A_{max} \sim \mathrm{Sex}, T_m \sim \mathrm{Sex}$	5	1459	1.5	0.2	1
	$A_{max} \sim 1, T_m \sim 1$	3	1462	4.7	0	1
2015	**$A_{max} \sim 1, T_m \sim \mathrm{Sex}$**	**4**	**1508**	**0**	**0.5**	**0.5**
	$A_{max} \sim \mathrm{Sex}, T_m \sim 1$	4	1509	0.9	0.3	0.8
	$A_{max} \sim \mathrm{Sex}, T_m \sim \mathrm{Sex}$	5	1510	2.1	0.2	1
	$A_{max} \sim 1, T_m \sim 1$	3	1589	80.8	0	1
2016	**$A_{max} \sim 1, T_m \sim \mathrm{Sex}$**	**4**	**1560**	**0**	**0.5**	**0.5**
	$A_{max} \sim \mathrm{Sex}, T_m \sim 1$	4	1561	0.8	0.3	0.8
	$A_{max} \sim \mathrm{Sex}, T_m \sim \mathrm{Sex}$	5	1562	1.7	0.2	1
	$A_{max} \sim 1, T_m \sim 1$	3	1680	121.1	0	1
2017	**$A_{max} \sim \mathrm{Sex}, T_m \sim 1$**	**4**	**1587**	**0**	**0.5**	**0.5**
	$A_{max} \sim 1, T_m \sim \mathrm{Sex}$	4	1587	1	0.3	0.8
	$A_{max} \sim \mathrm{Sex}, T_m \sim \mathrm{Sex}$	5	1589	2.1	0.2	1
	$A_{max} \sim 1, T_m \sim 1$	3	1639	52.7	0	1

to reach feeding areas under changing climatic conditions (i.e., wind speed and direction, visibility, etc.).

In general terms, for each year, the minimum sample size required to estimate the core foraging area was larger than that required for the active use area. This suggests that variability among individuals is greater in feeding zones than in transit zones. One possible explanation is that shags share transit routes from the colony to food patches, using similar environmental cues and/or acquiring information through the observation of conspecifics (Ward & Zahavi 1973, Weimerskirch et al. 2010, Regan et al. 2024). However, once in foraging areas, individuals tend to disperse, which would reduce intraspecific competition for food (Davoren et al. 2003). This pattern is consistent with that reported by Weimerskirch (2007), who analyzed trajectories from 34 seabird species and found that, at the population level, birds travel through similar zones toward feeding areas, although each individual shows some preference for specific sectors within them.

Table 6. Estimated parameters of the Michaelis–Menten model that showed the best fit for each year to predict core foraging area as a function of sample size for female and male Imperial shags (*Leucocarbo atriceps*) at the Punta León colony. The confidence interval [Min–Max] is indicated. Significant comparisons between sexes for the parameters A_{max} and T_m are shown in bold.

Year	A_{max}		T_m	
	Female core foraging area (km^2)	Male core foraging area (km^2)	Female core foraging area (*n* of animals)	Male core foraging area (*n* of animals)
2008	256 [158-354]	263 [187-340]	15 [6-23]	14 [8-20]
2009	**244 [151-337]**	**168 [120-217]**	16 [7-25]	11 [6-16]
2010	238 [139-337]	230 [152-309]	**18 [8- 28]**	**15 [7- 22]**
2013	**211 [98-324]**	**154 [103-206]**	21 [6-36]	15 [7-22]
2015	206 [139-274]	205 [106 -305]	**14 [7-20]**	**20 [7-33]**
2016	196 [154-239]	171 [123 -220]	**9 [5-12]**	**12 [7 -17]**
2017	**245 [178-313]**	**197 [131- 263]**	13 [7-18]	12 [6-19]
Mean	228 [196-256]	199 [103-187]	15 [9-21]	14 [11-20]

In all seasons, the sizes of the active use and core foraging areas of both males and females increased with increasing sample size until reaching an asymptote. This pattern indicates that precise results can be obtained with a limited number of tagged individuals. The interannual variability observed in use and foraging areas suggests that, to determine areas of activity, it may be more appropriate to maintain an adequate number of tagged individuals over the long term rather than tagging a very large number in only a few seasons. In any case, the number of males and females to be tagged will depend on previous evidence reporting differential space use—and/or behaviors that lead to it—between sexes.

In our case, under the 1% criterion, we found that 25 and 32 tagged individuals per sex (i.e., approximately 0.4–0.5% of the total number of breeding adults of each sex in the colony) would be necessary to estimate the sizes of the active use and core foraging areas, respectively, with that level of precision. The numbers of animals to be tagged are reduced to less than half (i.e., 10 and 12, for use and foraging areas, respectively) if a precision level of 5% is considered acceptable for determining area size. The choice of which precision level to adopt will depend on the accuracy required by the conceptual and/or experimental framework of the research and, ultimately, on the time and financial resources available. Conceptually complex questions may require the 1% criterion, that is, the highest level of precision, and therefore a larger number of tagged birds. However, for exploratory studies or for identifying areas of importance (e.g., IBAs), the 5% criterion would allow optimization of time and financial resources allocated to device acquisition without substantially compromising the representativeness of the study.

It is important to consider that the results obtained in this study focus on a particular period of the breeding season and on a specific site; therefore, extrapolation to other sites and/or periods of the same species or to other similar species should be made with caution. Likewise, results obtained from estimates for sample sizes greater than the reference sample size should be interpreted carefully. The reliability of the model describing the relationship between area size and number of individuals decreases once the sample size used in the present study is exceeded (20 Imperial shags for the population-level analysis and 10 for the sex-specific analysis). Extrapolations beyond these values are based on model predictions, which involve a higher degree of uncertainty (Colwell et al. 2012).

The implementation of GPS devices and related technologies in wildlife studies does not always include an adequate assessment of their impacts on animal welfare (Quintana et al. 2024). In this context, the careful planning of instrumentation strategies constitutes not only a measure of scientific efficiency—by optimizing resources and reducing sampling and analysis time—but also a commitment to fundamental ethical principles by avoiding excessive and unnecessary handling. This study seeks to contribute to the development of more responsible scientific practices by promoting the conscious and justified use of biologging devices.

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