Scientia Marina 89(1)
March 2025, e093
ISSN-L: 0214-8358, eISSN: 1886-8134
https://doi.org/10.3989/scimar.05550.093

Prey type and prey size selection in a Eurasian oystercatcher population at the edge of its distribution range

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Summary: This study targeted prey type and prey size selection by a small but expanding population of the Eurasian oystercatcher (*Haematopus ostralegus*) at the southernmost range of its European distribution (Galicia, NW Spain). We compared consumption and availability of prey items delivered to chicks. Consumption was studied through piles of discarded shells and availability was sampled in the foraging grounds located around nesting sites on three different islets. The only two prey types present in shell piles were mussels (*Mytillus galloprovincialis*) and limpets (*Patella* sp.). Our chi-square analyses did not detect any prey type selection by oystercatchers, but the use of the Savage index with Manly's method identified negative selection of limpets at one of the study sites. As a rule, the birds consumed limpets and mussels in proportion to their availability in their foraging grounds. At one of the study sites periwinkles (*Littorina* sp.) were present but not consumed. Regarding prey size, oystercatchers selected (1) mussels that were either similar to or larger than those available, and (2) limpets that were larger than those available. However, at one site out of three, the oystercatchers positively selected limpets of smaller size than those available. Hence, our results showed some heterogeneity among sites regarding prey type selection, but quite a consistent pattern of selection of larger prey. We suggest that oystercatcher foraging ecology is not explained solely by considering the balance between energy uptake and costs, but importantly by introducing additional variables such as the risk of chick predation, and current nesting as refugees on islets with no access to mainland beaches and sand dunes for breeding, where both adult and chick diet could be substantially different.

Keywords: edge population, Galicia, limpets, mussels, predation risk, refugees, shell piles, chick diet.

Selección de presa y de tipo de presa en una población de ostrero eurasiático en el límite de su área de distribución

Resumen: Este estudio analiza la selección del tipo de presa y del tamaño de presa por parte de una población pequeña, pero en expansión del ostrero euroasiático (*Haematopus ostralegus*) en el área más meridional de su distribución europea (Galicia, noroeste de España). Comparamos el consumo y la disponibilidad local de las presas proporcionadas a los pollos. El consumo se estudió a través de concheros y la disponibilidad se muestreó en las zonas de forrajeo ubicadas en el entorno de los sitios de nidificación, en tres islotes diferentes. Los únicos dos tipos de presa presentes en los concheros fueron mejillones (*Mytillus galloprovincialis*) y lapas (*Patella* sp.). Nuestros análisis mediante Chi-cuadrado no detectaron ninguna selección del tipo de presa por parte de los ostreros, pero el uso del índice de Savage, con el método de Manly, identificó una selección negativa de las lapas en uno de los sitios de estudio. Como regla general, las aves consumieron lapas y mejillones en proporción a lo que estaba disponible en sus zonas de alimentación. En uno de los sitios de estudio se encontraron bígaros (*Littorina* sp.) pero no fueron consumidos. En cuanto al tamaño de las presas, los ostreros seleccionaron (1) mejillones que eran similares o más grandes que los disponibles, y (2) lapas que eran más grandes que las disponibles. Sin embargo, en uno de los tres sitios, los ostreros seleccionaron positivamente lapas de menor tamaño que las disponibles. Por lo tanto, nuestros resultados mostraron cierta heterogeneidad entre sitios en cuanto a la selección del tipo de presa, pero un patrón bastante consistente de selección de presas grandes. Finalmente, sugerimos que la ecología de alimentación de los ostreros no se explica únicamente considerando el balance entre la adquisición de energía y los costes, sino que también intervienen variables adicionales, como el riesgo de depredación de los pollos y el hecho de que actualmente los ostreros estén refugiados en islotes sin acceso a playas y dunas de arena continentales para la reproducción, donde tanto la dieta de los adultos como la de los pollos podrían ser sustancialmente diferentes.

Palabras clave: población borde, Galicia, lapas, mejillones, riesgo de depredación, refugiados, concheros, dieta de los pollos.

Citation/Como citar este artículo: Ron Arroyo N., Mouriño J., Bermejo A., Rodríguez-Silvar J., Martínez-Abraín A. 2025. Prey type and prey size selection in a Eurasian oystercatcher population at the edge of its distribution range. Sci. Mar. 89(1): e093. https://doi.org/10.3989/scimar.05550.093

Editor: D. Oro.

Received: May 24, 2024. **Accepted:** October 24, 2024. **Published:** March 28, 2025.

INTRODUCTION

The study of prey and prey size selection helps us better understand ecological interactions between predator and prey, and their possible influence on the structuring of food webs and prey communities (Pokharel 2020). The decision of what and where to forage is guided theoretically by the strategy of optimizing energy acquisition by unit of time, as analysed by optimal foraging theory (Fargallo et al. 2020, Strandmark 2024). However, fitness factors other than the balance between energy acquisition and costs may also play a role, as will be discussed below.

Oystercatchers are known to be quite plastic regarding prey type choice, consuming the most abundant prey at each coastal site (Tjørve and Tjørve 2010). In fact, when they colonize inland territories far from the coast, their diet can shift to terrestrial prey (van de Pol et al. 2014). Additionally, the selection of prey items by oystercatchers may also be influenced by parameters that determine the cost/benefit ratio, such as size, thickness of the valve, pulp content, presence of barnacles on the valves and seasonal differences in available sizes (Hilgerloh and Pfeifer 2002, Rossignol et al. 2011). Many studies have approached prey size selection by the Eurasian oystercatcher (see e.g. Cayford and Goss-Custard 1990, Zwarts et al. 1996), reporting a wide range of results depending on the physical and ecological characteristics of each study site. However, Hilgerloh and Pfeifer (2002) suggested the existence of a preferred mussel size for oystercatchers, so that if the size class which seemingly optimizes the benefit/cost relationship is not available, oystercatchers would then try to forage on mussels as close in size to it as possible, if costs or time constraints are not too demanding.

The Iberian Peninsula represents the southernmost limit of the distribution of Eurasian oystercatchers (*Haematopus ostralegus*) in the western Palearctic, along with the populations of the Greek and Turkish peninsulas. Populations located at the limit of their distribution range may have different vital rates and foraging ecology to those of populations located closer to the centre of the distribution range of the species, tending to be more vulnerable to environmental stochasticity due to their small size, and to local extinction due to a poor rescue effect when distance to population cores is great (Van Schmidt and Beissinger 2020). Hence, the study of edge populations should be considered a conservation priority (see e.g. Martínez-Abraín et al. 2019A, 2023) despite the overall conservation status of the species, which in Europe is Near Threatened in the case of *H. ostralegus* (BirdLife International 2019).

In the Iberian Peninsula, oystercatcher populations have experienced a decline in the northeast (Ebro Delta), showing a 4% annual decrease during the period 2001-2020. On the other hand, northwestern Iberian populations (Galicia) have progressively increased (Rías Baixas) or remained stable (Lugo coast) over the last few decades (Mouriño et al. 2021). The oldest colonies in NW Spain are located in abrupt coastal islets where nesting oystercatchers have found an ecological refuge in the last few decades (Mouriño et al. 2021). However, human rural flight during the last 60-70 years has allowed oystercatchers to colonize or recolonize small flat islets (Fig. 1). These sites are easily accessible by humans and remained unoccupied by gulls and oystercatchers until recently due to permanent human disturbance (see Martínez-Abraín et al. 2019b, 2021). They constitute a suboptimal alternative to beaches and dunes, which are locally occupied by people and thus largely unavailable to wildlife, unlike the Ebro Delta colony in NE Spain where beaches and dunes are protected (Fig. 1). This forced nest site selection (anthropogenic forcing) is expected a priori to influence foraging behaviour due to factors unrelated to foraging preference or edge-of-distribution-related effects (ecological forcing), a fact that is often overlooked in studies of prey and prey size selection.

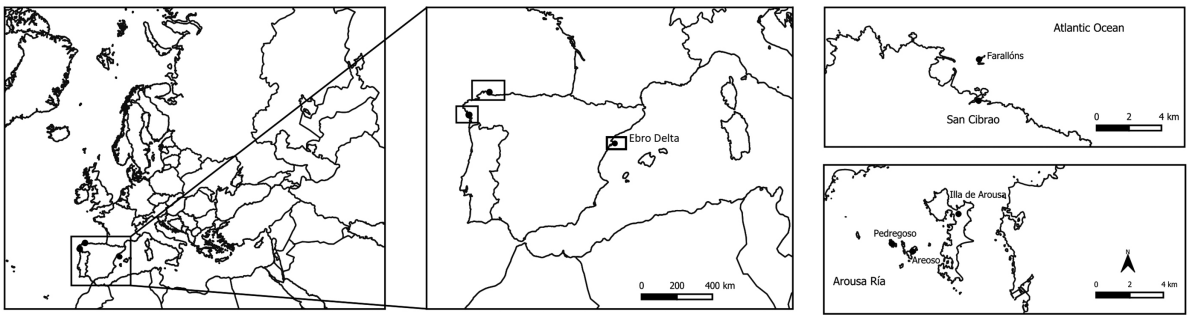

Fig. 1. - Location of the three study sites within the context of the Iberian Peninsula and western Europe. We also show the location of the Ebro Delta colony in the Iberian Mediterranean, which was until recently the only colony of the species in Iberia.

Here we analyse for the first time whether the expanding breeding populations of Eurasian oystercatcher from NW Spain show a preference for any prey type or prey size (for chick feeding) on three small flat islets in which the species has nested syntopically with yellow-legged gulls (*Larus michahellis*) during the last few decades. Based on current knowledge, our a priori expectations were that oystercatchers would show high foraging plasticity, with no selection of prey type but a tendency to select larger, more profitable prey sizes.

MATERIAL AND METHODS

Study sites

We sampled three small breeding sites of the Eurasian oystercatcher in Galicia (Fig. 1) consisting of small flat islets with a variable proportion of exposed rock outcrops and sand deposits. Two of them (Areoso and Pedregoso) are located in Ría de Arousa (Galician western coast). Areoso (ca. 9 ha.) has extensive but low-lying sand dunes and a rocky strip in the outer part deprived of vegetation, with four oystercatcher breeding pairs in 2023 and nesting recorded since 2013. It is located 1.5 km off Illa de Arousa, a large island communicated with the mainland by means of a large bridge. Pedregoso (5.6 ha) is a rocky islet with very scant beaches and sand dunes. Oystercatchers have been breeding on Pedregoso since 2010, with two pairs in 2023. It is located 2.8 km off the coast of Illa de Arousa. Locally, Areoso and Pedregoso are known collectively as Os Guidoiros islets. The third site (Farallóns islets, 5.8 ha) is located further north on the north coast of Galicia. It has had 3-4 breeding pairs of oystercatchers during the last 40 years, including 2023 (J. Mouriño, own unpublished information). It is located closer to the coast (1.5 km from the continental coast in San Cibrao) and is composed of exposed rock with very scant salt-marsh vegetation. The three islets belong to different special protection areas for birds.

Field data collection

To study prey consumption, prey availability and prey size, Areoso, Pedregoso and Farallóns were each sampled once, on 17 July 2020, 16 July 2021 and 2 July 2022, respectively. All samplings were carried out at low tide to be able to determine prey availability in adjacent foraging grounds. The samplings were performed during the month of July, taking into account the local breeding calendar of the species and the need to avoid overlapping with the most vulnerable period of its reproduction (egg incubation in May). We took advantage of the fact that piles of discarded shells were generated at high-tide spots after molluscs were eaten most likely for chick feeding, so remains were found concentrated on small patches of bare rock (approximately 4×4 m in our case; Fig. 2). This probably happens because chicks were hidden in high-tide-safe sheltered points, and this fortuitously led to the formation of the dense piles of discarded shells close to them as a by-product when adults bring food onshore to feed the chicks. The mussels were opened in half in a vertical plane by the oystercatchers, and hence the valves were complete. Limpets were not found broken either, but just as whole shells detached from the rock. We first searched for piles of discarded shells on each islet. Mussel valves were assumed to come from independent individual

mussels regardless of whether they were left or right valves. This may have introduced some unknown degree of bias in favour of mussels on the islet where mussels were relatively common (Areoso), although it is certainly not relevant because no positive selection of mussels was detected (see Results section). Prey availability was sampled in foraging areas adjacent to breeding areas because previous observations (A. Bermejo, J. Mouriño, X. Silvar, own unpublished information) indicated that breeding oystercatchers forage in the vicinity of breeding colonies during low tide on the study islets. This finding is consistent with the short foraging excursions reported by Tjørve and Tjørve (2010), although this is not the case for all populations (Leopold et al. 1996). The study of consumed prey was performed by launching a wire square (40×40 cm) blindly two to three times on top of the discarded shell piles. We counted the number of shells of each prey type found within the squares. We measured the width and length of the prey found within the squares using a Mitutoyo digital caliper, to the nearest 0.01 mm. We also measured the length and width of prey items found in our samplings of prey availability. To study prey availability, we launched the wire square overhead on the foraging grounds at low tide. The square was launched backwards by different observers to avoid launching biases such as aiming unconsciously for areas with larger-size prey (i.e. sampling was randomized). A total of 12 launches were performed in Areoso, 10 launches in Farallóns and 4 launches in Pedregoso. The number of launches performed was smaller on Pedregoso than on the other two islets because an initial visual inspection of the area showed an overall scarcity of mussels. Additionally, the sampling of prey availability was stopped in the fourth launch because there was a large number of limpets within the limits of the wire square, providing a large enough sample size to determine mean limpet size. Increasing the number of square launches would have not changed the proportion of mussels. However, we must acknowledge some unknown degree of bias in the determination of limpet length if limpet size is not independent within quadrats.

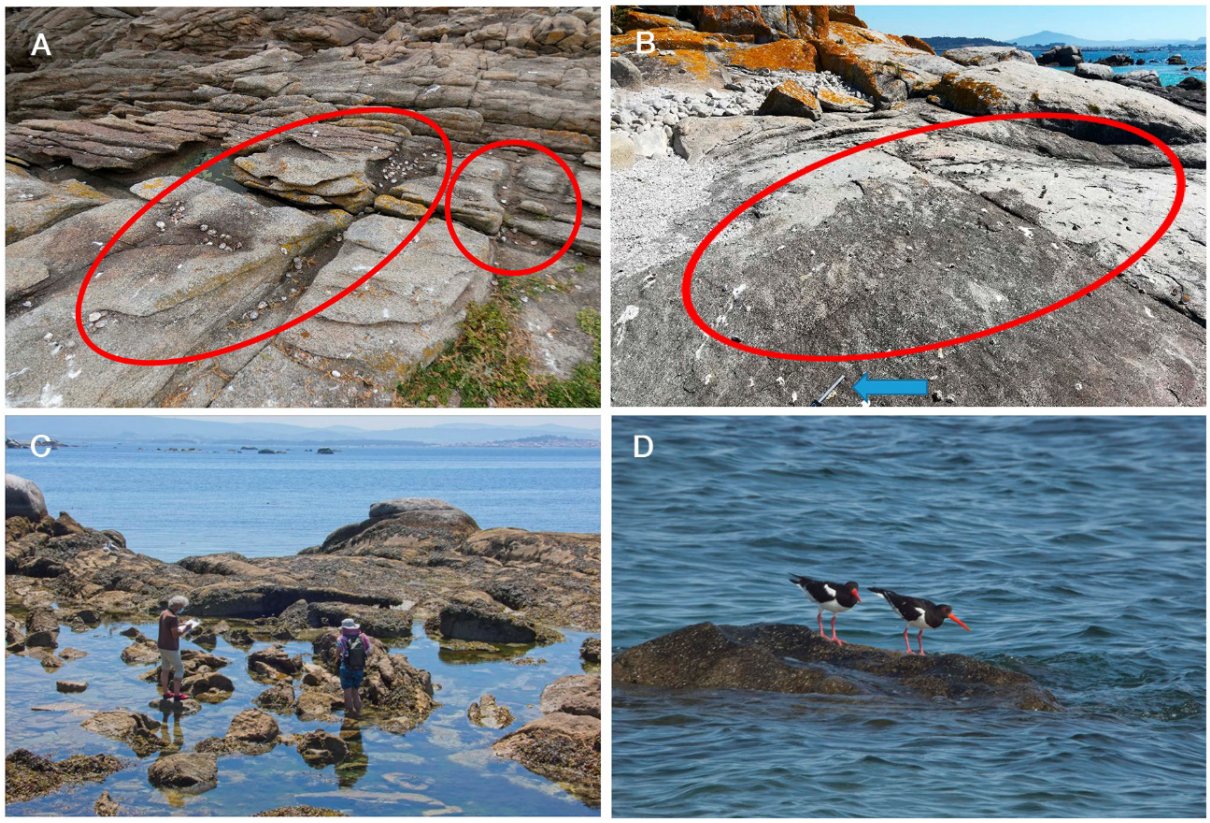

Fig. 2. - A, discarded shell pile on Farallóns islet. B, discarded shell pile on Pedregoso islet (note the digital caliper in the lower left corner for scale, blue arrow). C, sampling of available prey in foraging grounds at low tide on Pedrogoso islet. D, oystercatcher pair at high tide in foraging grounds (image credits: Xan Silvar).

Statistical analyses

We first performed parametric correlation analyses (Pearsons's r) between the length and width of shells to assess collinearity. Since all correlations were positive, strong and statistically significant (r=0.95, 95% CI 0.92-0.96 for one prey type and r=0.91, 95% CI 0.89-0.93 for the second prey type), we decided to work only with the length variable for the study of prey size selection. We estimated the arithmetic mean and standard deviation of shell length in both prey types.

Normality was assessed by means of Kolmogorov-Smirnov tests. A logarithmic transformation of data was carried out when we detected departures from normality. Barlett's test for the homogeneity of variances was also conducted for each variable. Student's t test for unequal variances (Welch's test) was used when necessary. Otherwise, we used ANOVA to look for differences in mean prey length between consumed and available prey.

To check whether oystercatchers had a preference for any of the two prey types detected, 2x2 contingency tables were set up. Subsequently, a chi-square test was applied, with Yates's correction for small samples, and the standardized residuals of the test were studied to quantify the departure of observed from expected frequencies. Additionally, to determine the selection of prey by means of a second method, the value of the Savage index, following Mainly's method (Mainly et al. 1993), was also computed. The values of this index range between 0 (maximum negative selection) and infinite, 1 being the central value of no selection (Chesson 1978, Lechowicz 1982, Atienza 1994). All analyses were carried out using R 4.2.2 software (https://www.r-project.org).

RESULTS

Prey type selection

The only two prey types present in shell piles were mussels (*Mytillus galloprovincialis*) and limpets (*Patella* sp.). We counted a total of 51 consumed mussels and 176 consumed limpets (see Table 1 for allocation per islet). Additionally, we counted a total of 43 mussels and 169 limpets in our sampling of prey availability (Table 1).

Table 1. - Mean length and standard deviation of consumed and available oystercatcher prey (mussels and limpets) in the three study locations and qualitative conclusions from our statistical analyses of differences in mean length. Cohen's d is also shown as a metric of effect size.

	Consumed (mm)	Available (mm)	Size selection	Direction	Cohen's d
		Mussels			
Areoso I.	47.55±8.98 (n=34)	30.64±6.53 (n=35)	Yes	Larger	0.262
Pedregoso I.	49.32±4.89 (n=17)	49.58±7.38 (n=8)	No	Similar	0.006
Farallóns I.	Not present	Not present	---	---	---
		Limpets			
Areoso I.	41.44±8.75 (n=36)	37.02±12.25 (n=60)	Yes	Larger	0.037
Pedregoso I.	33.57±5.41 (n=44)	41.86±7.54 (n=46)	Yes	Smaller	0.183
Farallóns I.	29.33±5.36 (n=96)	25.06±5.14 (n=63)	Yes	Larger	0.154

Our chi-square analyses did not detect any prey type selection by oystercatchers (χ^2 =1.82, df=1, P>0.05 in Areoso, and χ^2=2.15, df=1, P>0.05 in Pedregoso). That is, the birds consumed limpets and mussels in proportion to what was available in their foraging grounds, next to their nesting sites. Consequently, residuals of the chi-square tests were small (0.87 for consumed mussels and -0.74 for consumed limpets in Areoso; 1.03 for consumed mussels and -0.54 for consumed limpets in Pedregoso), indicating that observed frequencies were quite similar to expected frequencies.

Values of the Savage index of selection on Areoso were 1.30 and 0.80 for mussels and limpets, respectively. Mainly's method indicated that there was no prey type selection regarding mussels or limpets. The values of the Savage index were 1.82 for mussels and 0.85 for limpets on Pedregoso. However, the use of the Savage index with Mainly's method indicated the existence of negative selection in relation to limpets (i.e. limpets were consumed in a lower proportion than expected due to their abundance). Based on the results from both the chi-square tests and the Savage index for the three islets, we can state that mussels were consumed in proportion to their abundance (no selection), whereas limpets were either consumed in proportion to their availability (no selection) or were negatively selected.

Prey size selection

Our analyses showed statically significant differences in mean length between consumed and available mussels from Areoso (ANOVA=80.27=61, $P<0.05$; $n=69$), where oystercatchers selected mussels that were larger than those available. However, we were unable to find statistically significant differences in mean length between consumed and available mussels on Pedregoso (ANOVA=0.011=33.24, $P>0.05$; $n=25$), where oystercatchers preyed on available mean mussel sizes (Table 1).

Regarding limpets, our analyses showed statically significant differences between the mean length of consumed and available limpets in all locations. On Areoso (t=2.05, df=91.05, $P<0.05$; $n=96$) and Farallóns (t=5.03, df=136.71, $P<0.05$; $n=159$) oystercatchers preyed on limpets that were larger than those available, but on Pedregoso oystercatchers chose limpets that were smaller than the mean limpet size available (t=6.02, df=81.757, $P<0.05$; $n=90$) (Table 1).

DISCUSSION

Based on our results, we cannot conclude the existence of clear positive or negative selection of one prey type over another. Although the values of the Savage index pointed to some preference for foraging on mussels over limpets, the null selection hypothesis was only statistically rejected for limpets on Pedregoso (negative selection). These results coincided with what was expected a priori, because previous studies found that oystercatchers choose the prey types that are most abundant within breeding territories (e.g. Tjørve and Tjørve 2010). On Farallóns, we were unable to study prey selection because mussels were not available in the colony or present in shell piles. All consumed prey were limpets. Since shells remain in the shell piles for a long time, it is unlikely that the absence of valves in the foraging ground means that oystercatchers had already consumed all mussels available and that our results have validity only for a short time window. Additionally, we recorded the presence of periwinkles (*Littorina* sp.) on Farallóns (in seven out of the ten squares sampled in the foraging grounds), but this mollusc was not found in shell piles, suggesting a negative selection of this species, which would be consistent with the findings reported by Tjørve and Tjørve (2010) in Norway. However, this species was not included in our study because it was not present in shell piles or sampling squares on Areoso and Pedregoso that were sampled prior to Farallóns.

In summary, the results of our study showed heterogeneity among sites in prey type, supporting the idea that oystercatchers may act as facultative specialists, foraging on the most common prey at each site without showing a clear preference for one prey type or another. Only the negative selection of limpets on Pedregoso suggested that oystercatchers may forage on limpets in a lower proportion than expected by its abundance in the local environment. This foraging plasticity has applied conservation consequences because it is easier for facultative specialists to expand and colonize new sites, as this is actually happening with this species in Atlantic Iberia.

Regarding prey size selection, our analyses detected selection for larger sizes in most cases: mussels and limpets on Areoso and limpets on Farallóns, consistently with the findings of most studies on prey size selection by the Eurasian oystercatcher (Drinnan 1958, Ens et al. 1992). However, Leopold et al. (1996) found that selection for the most profitable prey could increase chick predation risk, because adults had to remain longer away from colonies and, hence, they did not select for large prey size unless they had to travel long distances. Our study oystercatchers nested associated with yellow-legged gulls (265 and 88 gull pairs on Pedregoso and Areoso, respectively, in 2022; Dirección Xeral de Patrimonio Natural 2024) and great black-backed gulls (*Larus marinus*) (1 and 4 pairs on Pedregoso and Areoso, respectively, in 2023; J. Mouriño own unpublished data), all of them facultative oystercatcher predators (Tjørve and Tjørve 2010).

Nevertheless, we found that oystercatchers selected for larger prey to feed chicks, meaning that their foraging grounds had to be close to nesting sites (i.e. in exposed rocks at low tide around nesting areas, as previously observed by us), and thus that they were away from the proximity of chicks for short time periods. Moreover, our field observations of birds foraging in the Coelleira, Ansarón and Gaveira de Viveiro colonies (X.M. unpublished) support the need to minimize the risk of chick predation because the two adults of each nesting pair do not forage at the same time, but one of them remains in the vicinity of chicks until the second brings food for the chicks.

Additionally, we also detected selection for small size of limpets on Pedregoso but were unable to show selection for size of mussels there. The selection for smaller limpets could be due to lack of independence of the limpets measured, as a large number of them came from the same quadrat (for example, individuals could be affected by density dependence or be closely related to each other). Alternatively, this result could also be a consequence of adult oystercatchers foraging farther from colonies than usual, trying to minimize the time spent away from chicks. The lack of selection for mussels could simply be an artefact caused by low sample size (n=17 mussels consumed and n=8 available). Selection for smaller prey has only been previously found in studies in which the Eurasian oystercatcher's target prey was the common cockle (*Cerastoderma edulis*). However, the closely related African black oystercatcher (*H. moquini*) showed lack of discrimination of clam (*Donax serra*) size; there was temporal segregation of small and large clams but, even when large clams were abundant they took both small and large clams (Ward 1991). Moreover, if oystercatchers forage mainly on mussels from the upper limit of their size class distribution, they could also influence the composition of mussel size classes available in the long run, so only smaller size classes would be available (i.e. self-trophic downgrading regarding prey size occurred; Hamilton 2000). A similar effect is known to be caused by the anthropogenic preference for large prey in hunting and fishing (Soga and Gaston 2018). Prey of different sizes present different profitability for the predator, depending on the time required for prey handling and the meat content. As stated in the introduction, Hilgerloh and Pfeifer (2002) suggested that oystercatchers had an optimal median mussel size of 51 mm, and that when the mussels available were smaller than the ideal size, they selected the largest ones available. Interestingly, in our study the overall median length of consumed mussels was 46.86 mm (48.14±7.85; arithmetic mean±SD), close to 51.

As the study oystercatcher population is currently growing, with new colonies being established every year, further studies should be carried out in the future to confirm or amend these preliminary findings. Likely human influence on mussel availability due to collection of juvenile mussels for industrial mussel growth should also be explored within the framework of future plans for the conservation of this expanding oystercatcher population. This problem would be less important if oystercatchers could have access to protected mainland beaches and dune fields in the future for nesting and forage on different prey types (e.g. soft prey from sandy substrates).

ACKNOWLEDGEMENTS

We are most grateful to an anonymous referee and the associate editor (Daniel Oro) for his review of the submitted manuscript and his thoughtful suggestions to improve it. We are also very grateful to Pilar Santidrián and Pedro Galán, who commented on drafts of the manuscript. Pipo Sierra helped us to randomize the sampling of prey at Pedregoso.

FUNDING SOURCES

This study was linked to project ED431B 2024/23, by which the Xunta de Galicia funded our research group (GIBE).

AUTHORSHIP CONTRIBUTION STATEMENT

Nicolás Ron Arroyo: data curation; formal analysis; writing-original draft. **Jorge Mouriño:** investigation; data curation. **Xan Silvar:** investigation. **Andrés Bermejo:** investigation. **Alejandro Martínez-Abraín:** conceptualization; methodology; supervision; writing-reviewing and editing.

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