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Prey size selection of insular lizards by two sympatric predatory bird species

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Abstract. Size-related selection of insular lizards by two sympatric predatory bird species (Southern Grey Shrike and Eurasian Kestrel) was studied in an arid insular environment. The endemic lizard genus *Gallotia* was a key resource in the diet of both predators, constituting more than 50% of the total biomass. Shrikes captured smaller lizards than kestrels during all seasons (mean snout - vent length (SVL): 7.4 ± 1.9 vs. 9.4 ± 2.1 cm respectively), presenting a sequential use of lizard sizes and avoiding potential competition. On the other hand, shrikes and kestrels showed the same seasonal variation pattern, capturing the largest lizards during their breeding periods (spring). Considering lizard availability, shrikes displayed less selective predation than kestrels in all seasons. Shrikes positively selected the medium lizard size (SVL: 5-10 cm) during the nestling period, but negatively selected the small lizard size (SVL: < 5 cm) in autumn and winter, probably due to an explosion of juvenile lizards. Lastly, kestrels appeared to be more selective, negatively choosing the small lizard size but positively selecting the largest ones all the year round (SVL: > 10 cm).

Key words: Kestrel, *Falco tinnunculus*, Southern Grey Shrike, *Lanius meridionalis*, Tenerife Lizard, *Gallotia galloti*, feeding ecology, prey selection, Canary Islands

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INTRODUCTION

Potential food interference of an important key resource for two sympatric species could be minimised by the sequential use of this resource, for instance differences in circadian activity (Schoener 1974, Barrientos & Virgós 2006). The coexistence of coevolved species in a community is facilitated by the segregation of one or more niches (Schoener 1974, Chesson & Huntly 1997). Niche separation is often explained by differences in diet or feeding strategies (Julien-Laferriere 1999, Telfer & Bowman 2006). The reduction of food niche overlap is often possible by the use of different prey sizes, through food division by type or by segregation in foraging areas (Schoener 1974, García & Arroyo 2005, Barrientos & Virgós 2006). Competition theory predicts a high overlap in diets with low competition between sympatric species when a key prey resource is abundant (Lack 1946, Schoener 1982).

Several ecological phenomena describe how the species that inhabit island ecosystems often expand their niches and habitats, and exploit resources that are generally used by other species in continental environments (Whittaker & Fernández-Palacios 2007). The abundance of some animals, such as lizards, is often greater on islands than on the mainland, due to lower predation and competition pressure, or their broader trophic niche (Evans & Evans 1980, Brown et al. 1992, Olesen & Valido 2003). This is the case of the Canarian endemic genus *Gallotia*, which is represented by seven living lizard species (Nogales et al. 2001). These lizards differ in body sizes, ranging approximately between 6 and 25 cm in snout vent length (hereafter, SVL). Adult Tenerife Lizard *G. galloti* oscillates between a SVL of 10.7 and 14.5 cm. On this island, two birds are the main lizard predators, the Southern Grey Shrike *Lanius meridionalis* and the Eurasian Kestrel *Falco tinnunculus* (Martín & Lorenzo 2001) which breed

sympatrically in many areas. Both predatory birds are clearly different in size (shrikes: full length: 24–25 cm, weight: 62–63 g; kestrels: 34–38 cm and 155–225 g males; 230–270 g females), and all available evidence seems to indicate that a segregation in the predation of different lizard body sizes may be occurring in these insular environments.

In the Canary Islands, the diet of the Southern Grey Shrike is mainly made up of vertebrates, the endemic lizards *Gallotia* constituting 64% of the whole biomass (Padilla et al. 2005). In the case of the Eurasian Kestrel, the lizard biomass constitutes more than 50% of the total diet in many habitats of the archipelago (Carrillo et al. 1994, Martín & Lorenzo 2001). This high proportion of lizards in both shrike and kestrel diets is clearly related to the great abundance of these Lacertidae in island environments, the high effectiveness of predation and the low investment of energy in capturing this prey (Padilla et al. 2005).

The main aims of this study were: 1) to establish the importance of lizards in the diet of two sympatric birds of prey, the Southern Grey Shrike and the Eurasian Kestrel, 2) to determine the existence of differential predation upon different lizard sizes by these two predatory birds and, 3) to assess seasonal selective predation of lizard sizes in an arid environment of the Canary Islands.

MATERIAL AND METHODS

Study area

The volcanic Canary Islands are located in the Atlantic Ocean some 100 km from the African continent (27°37'–29°25'N, 13°20'–29°25'W). Fieldwork was carried out in “Malpaís de La Rasca” nature reserve and surrounding areas, located in the southernmost part of Tenerife. The study area consists in a recent lava field ($\approx 3.15 \text{ km}^2$) which was produced by two main volcanic cones, Montaña Gorda and Montaña Aguzada (Carracedo et al. 2003).

The climate is xeric, with a mean annual rainfall and temperature of 98 mm and $\approx 22^\circ\text{C}$, respectively (Marzol Jaén 1988). However, two climatic periods can be identified in this semiarid habitat: dry (spring and summer; mean rainfall and temperature of 11.2 mm and 22.5°C , respectively); and rainy (autumn and winter; 86.7 mm and 22.2°C). The vegetation consists of sparse xerophytic shrub, mainly composed of *Launaea arborescens*, *Lycium intricatum*, *Salsola divaricata*, *Schizogyne glaberrima*, *Euphorbia balsamifera*, *E. canariensis*,

Plocama pendula and the invasive *Opuntia dillenii* (Arco-Aguilar et al. 1997).

Pellet sampling

The study was performed from April 2003 to March 2004, this period being divided into four seasons (spring: March, April and May; summer: June, July and August; autumn: September, October and November; and winter: December, January and February). A total of 440 Southern Grey Shrike pellets were collected in fourteen territories (spring: 115, summer: 116, autumn: 93 and winter: 116); and a total of 486 Eurasian Kestrel pellets were taken in five different territories (spring: 141, summer: 141, autumn: 125, winter: 79). All kestrel territories overlapped with at least one shrike territory. A mean number of 10 shrike pellets and 30 kestrel pellets per territory and season were collected in order to have an adequate representation of both population diets. To minimize seasonal sample bias, only fresh pellets were collected after periodic cleaning beneath perches. We decided to use pellet samples, because well-preserved long bones are often found inside them. Moreover, we revised the shrike larders regularly and only five lizards were found, which due to their low number were not included in the analysis.

Pellet analysis and prey size

Each pellet was analysed individually, counting long bones (femoral, humeral, tibia, pelvic girdle and parietal) and mandibles or maxillaries of reptiles. Percentage of occurrence was calculated to evaluate the importance of lizards in the diet of both birds.

Length of lizards (Lacertidae, *Gallotia galloti*) main bones that appeared whole and well preserved inside pellets (jaws, maxillaries, parietals, pelvic girdle, femoral, tibias and humeri), were measured with a digital caliper to calculate body sizes. To minimise measurement bias, only one person recorded data. We used the respective regression models detailed by Nogales & Valido (1999) for *G. galloti*, which consist in relationships between lizard snout vent length (hereafter SVL) and the afore-mentioned main bones.

Gallotia galloti (SVL: 10.7–14.5 cm) is present in all habitats of Tenerife and it is the only lizard that lives in the study area (Hernández et al. 2000). To study prey size selection, the relative abundance of lizards was calculated in “Malpaís de La Rasca”, using line transects (100 m length) located inside those predatory bird territories studied; all lizards

that appeared up to five meters on both sides of the observer were counted (Díaz & Carrascal 1990). Censuses were made between 12:00 and 14:00 hours (maximum activity period of lizards), on fair days and a total of 20 transects were performed in each season. To ascertain if the Southern Grey Shrike and the Eurasian Kestrel were selecting specific lizard sizes, these were classified in three different categories (small: SVL < 5 cm; medium: SVL 5–10 cm; and large: SVL > 10 cm).

Statistical and index analysis

To compare the sizes of lizards captured during the annual cycle, a shrike *versus* kestrel t-student test was employed. Chi-square tests were performed to evaluate the consumption of different lizard prey sizes by each species all year round. Likelihood ratio tests were used to find out if any lizard size category was consumed more frequently in a particular season. To study seasonal differences in lizard body sizes that appeared inside each predatory bird pellet, we used parametric tests (ANOVA and Sheffé post-hoc) and non-parametric tests (Kruskal-Wallis and Mann-Whitney) for those data in which distribution did not meet the requirements of a parametric test, even after transformations (Siegel 1990). In those cases where it was necessary to use the same data set, we reduced this effect by applying a more conservative sequential Bonferroni test.

To evaluate diet selection of lizard sizes, the “forage index” of Savage (1931) was applied, followed by the method proposed by Manly et al. (1993). For further details on the use of this index see Padilla et al. (2005).

RESULTS

In “Malpaís de La Rasca” the percentage of occurrence of lizards inside pellets revealed the great importance of this prey in shrike and kestrel diets (Shrike, spring: 39.1%, summer: 30.2%, autumn: 24.7%, winter: 31%; Kestrel, spring: 75.9%, summer: 69.5%, autumn: 66.4%, winter: 30.4%).

Kestrels captured significantly larger lizards than shrikes all year round (SVL; 9.4 ± 2.1 and 7.4 ± 1.9 cm, respectively; $t = 6.80$, $df = 175$, $p < 0.001$). The medium lizard size category was the most frequent prey captured all year round by shrikes ($\chi^2 = 77.5$, $df = 2$, $p < 0.001$), while in the case of kestrels the medium and large lizard sizes

were the most frequent prey captured ($\chi^2 = 44.21$, $df = 2$, $p < 0.001$) with no significant difference between them ($\chi^2 = 3.4$, $df = 1$, $p = 0.062$). A seasonal variation in lizards SVL was observed in each bird of prey (Shrikes: Kruskal-Wallis, $\chi^2 = 11.4$, $df = 3$, $p = 0.01$; Kestrels: ANOVA, $F = 4.4$, $df = 3$, $p = 0.006$). The same seasonal pattern was observed in both shrikes and kestrels; the only difference recorded being between spring and summer and, the largest lizards being captured in spring (Shrike: Mann-Whitney, $U = 276.5$, $p = 0.003$; Kestrel: Scheffé test, $p = 0.014$) (Fig. 1).

Prey size selection upon different lizard sizes by two sympatric birds of prey was calculated, observing scarce selection by shrikes. This species positively selected medium sizes (SVL 5–10 cm) in spring, whereas small lizards (SVL < 5 cm) were negatively selected in autumn and winter. The largest (SVL > 10 cm) appeared as negatively selected prey in summer, but were positively selected in autumn (Table 1). Kestrels, avoided capturing small lizards all year round, and they only appeared in those pellets collected in summer, showing a clear negative selection. In contrast, the largest lizard size was positively selected by kestrels all year round with the exception of summer when no selection was recorded (Table 1).

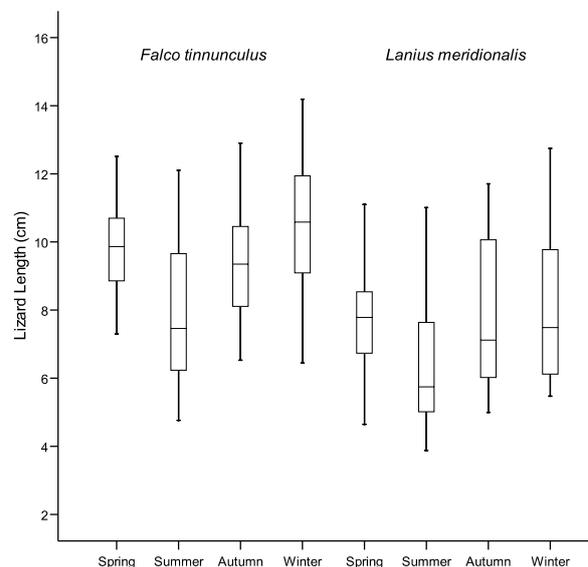


Fig. 1. Lengths (SVL) of lizards captured by the Eurasian Kestrel and the Southern Grey Shrike, in each season in Tenerife, Canary Islands. The box indicates the mean (\pm SD), the bars extending above and below each box illustrate maximum and minimum values.

Table 1. Selection of lizard body size depredated by Southern Grey Shrike and Eurasian Kestrel using in "Malpaís de La Rasca", Tenerife, Canary Islands the "forage index" of Savage (1931) and following the method proposed by Manly et al. (1993). SVL — snout vent length, PA — proportion of lizard availability in Malpaís de La Rasca, MS — values of the Manly statistic, DS — diet selection, S+ — positive selection, S- — negative selection, NS — no selection.

Lizard prey size (cm)	Spring						Summer						Autumn						Winter											
	Shrike		Kestrel		PA		Shrike		Kestrel		PA		Shrike		Kestrel		PA		Shrike		Kestrel		PA		Shrike		Kestrel		PA	
	MS	DS	MS	DS	MS	DS	MS	DS	MS	DS	MS	DS	MS	DS	MS	DS	MS	DS	MS	DS	MS	DS	MS	DS	MS	DS	MS	DS	MS	DS
Small (SVL < 5)	10	1.5	NS	-	S-	23.6	0.006	NS	3.9	S-	41.4	5.4	S-	-	S-	25.9	4.2	S-	-	S-	-	S-	-	S-	-	S-	-	S-	-	S-
Medium (SVL 5-10)	61.3	6.2	S+	1.3	NS	56.4	2.4	NS	2.8	NS	51.7	1.1	NS	0.6	NS	66.7	1.3	NS	0.8	NS	66.7	1.3	NS	0.8	NS	66.7	1.3	NS	0.8	NS
Large (SVL > 10)	28.8	3.5	NS	6.9	S+	20	4.0	S-	0	NS	6.9	6.1	S+	28.7	S+	7.4	1.9	NS	15.9	S+	7.4	1.9	NS	15.9	S+	7.4	1.9	NS	15.9	S+

DISCUSSION

In "Malpaís de La Rasca", the presence of lizards in the diet of the Southern Grey Shrike and the Eurasian Kestrel was very important. This high level of predation could be attributed to the fact that lizards reach high densities in the Canary Archipelago as a consequence of the lower pre-dation risk compared to the mainland (Olesen & Valido 2003). According to previous hypotheses on competition, when an important resource in the diets of two sympatric species is abundant, a high overlap between them would occur as an indicator of relaxed competition (Lack 1946, Schoener 1982, Gerstell & Bednarz 1999).

The best strategy for a predator is to acquire the greatest net energy per unit expended, and this could be related to the prey size ratio (Craig 1978). Moreover, birds of different body size could differentially use the dietary niche (Hromada et al. 2003). During all seasons, shrikes captured smaller lizards than kestrels, the most frequently captured prey in their diets being the medium and the medium-large size categories, respectively. This would suggest that the smaller predator (the shrike) has limitations in the capture and management of large lizards. Different studies have demonstrated how shrikes selectively capture small or medium vertebrate sizes and reject larger ones, which can be considered a trade-off between prey size and the expenditure of energy in transportation and handling (Yosef 1993, Hernández 1995, Probst et al. 2003). Furthermore, species with similar diets but different body mass require different net energy which is positively correlated with the amount of food required (Julien-Laferriere 1999, García & Arroyo 2005). Thus, studies on the diet of predatory birds, such as the American Kestrel *Falco sparverius* or the Eurasian Kestrel, have demonstrated how they preferred to prey on large lizards rather than on smaller ones (McLaughlin & Roughgarden 1989, Martín & López 1996, Costantini et al. in press). However, there are other predatory species, for instance the Kookaburras *Dacelo novaeguineae*, which prey mainly on small and medium-sized skinks (Blomberg & Shine 2000). In "Malpaís de La Rasca", kestrels might acquire more food than shrikes by concentrating on the largest lizards. In this lava field, kestrels and shrikes use different hunting strategies (pers. obs.). Kestrels regularly employed flight-hunting methods while shrikes are considered to be a "sit-and-wait" predator. The

former technique is the more energetically expensive (Masman et al. 1988) and, thus, kestrels have to select the most profitable prey (largest lizards) avoiding smaller ones.

Seasonal variation patterns were similar between the two birds of prey. In both cases, significant differences were observed between spring and summer. Both predators chose the largest lizards in the former season, coinciding with their breeding periods. In this season their respective offspring increase the demand for food, making this a stringent period for the parents since they have to dedicate most of their time to parental care and they could concentrate on a specific prey size (Costantini et al. 2005).

With respect to selective predation, the Southern Grey Shrike presented a scarce selection on lizard size, showing a certain tendency towards opportunistic behaviour (Table 1). However, in spring, coinciding with the nestling period, medium lizard size (SVL 5–10 cm) was positively selected. In contrast, in autumn and winter, when an explosion of juvenile lizards occurred (small size; SVL < 5 cm) they were negatively selected. On the other hand, kestrels showed a more selective behaviour than shrikes, clearly negatively selecting the small lizard size all year round and positively selecting the larger ones. Shrikes and kestrels presented similar patterns in lizard choice only in autumn and winter. In this period, energy expenditure is minimised because they are not breeding, and can probably spend more time selecting the most profitable food by rejecting smaller lizards.

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STRESZCZENIE

[Selekcja na wielkość zdobyczy sympatrycznie występujących srokosza i pustułki]

Badania prowadzono od kwietnia 2003 do marca 2004 w południowej części Teneryfy (3.15 km², Wyspy Kanaryjskie), gdzie współwystępują dwa gatunki drapieżników polujących głównie na drobne gady — srokosz i pustułka. Ich ofiarami na terenie objętym badaniami padają przede wszystkim endemiczne jaszczurki z gatunku *Gallotia galloti*. Zebrano 440 wypluwek srokosza (115 wiosną, 116 latem, 93 jesienią i 116 zimą) oraz 486 wypluwek pustułki (odpowiednio 141, 141, 125 i 79). Wszystkie terytoria pustulek z jakich pozyskano materiał pokrywały się z przynajmniej jednym terytorium srokosza. Oprócz tego szacowano liczebności jaszczurek na transektach i klasy wielkości widzianych osobników. Wyizolowane z wypluwek kości jaszczurek były mierzone, by oszacować wielkość ofiar.

Udział szczątków jaszczurek w wypluwkach pustulek zmieniał się w ciągu roku (od 75.9% wiosną do 30.4% zimą) i pozostawał mniej więcej stały w wypluwkach srokosza (24.7–39.1%). Pustułki chwyciły większe ofiary niż srokosze przez cały rok, przy czym srokosze wybierały jaszczurki należące średniej klasy wielkości. Pustułki chwyciły jaszczurki średnie i duże. U obu gatunków stwierdzono różnice między sezonami (Fig. 1). Wykazano, że w przypadku srokosza, drapieżniki dokonywały pozytywnej selekcji ofiar średniej wielkości na wiosnę, zaś negatywnej małych jaszczurek jesienią i zimą. Największe jaszczurki były unikane latem, natomiast chwytane jesienią. Pustułki unikały chwytania małych ofiar przez cały rok, ta grupa pojawiała się tylko w wypluwkach znajdujących latem, co wskazuje na zdecydowanie negatywną selekcję (Tab. 1).