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The Macaronesian Sparrowhawk diet in native and exotic forests

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The Macaronesian Sparrowhawk (*Accipiter nisus granti*) is an endemic subspecies restricted to the forest habitats of Madeira and the Canary Islands. We studied its inter-habitat diet variation on the largest of the Canaries, Tenerife, during the 2014–2015 breeding seasons. We also compared the current food spectrum (2014–2015) with that reported in a study conducted 30 years ago. Prey remains analyses were conducted at the three main forested habitats, two native (laurel forest and Canarian pinewood) and one exotic (exotic tree plantations). Birds formed the main dietary component of the Sparrowhawk (26 species identified), but mammals and reptiles were also consumed in small numbers. Avian prey of around 200–300 g were preferred by Sparrowhawks. Three species accounted for 63.4% of the total number of prey counted (Atlantic Canary *Serinus canarius*, Rock Pigeon *Columba livia* and Blackbird *Turdus merula*), but their importance varied among habitats. In laurel forests and exotic tree plantations diet niche breadth and prey diversity was greater than in the Canarian pinewoods as reflected by prey densities. A comparison of our data with those from 1984–85 showed that large-sized avian prey might have become more important in the diet spectrum and thus indicating changes in the population status of prey species. The majority of Macaronesian Sparrowhawk hunting habitats are exposed to agricultural and forestry practices that could result in negative population trends of Sparrowhawk prey. Further studies are required to fully understand predator-prey relationships and to develop effective management actions to guarantee the long-term conservation of this island raptor.

1. Introduction

Spatial and temporal understanding of diet variation and foraging strategies of top predators, such as raptors, is a crucial issue in ecology and conservation. Because of their position in food-webs, prey abundance is often a limiting factor for breeding density and reproductive performance, and thus, raptors are used as indicators of ecosystem health (Francksen *et al.* 2017, Kettel *et al.* 2018, Salafsky *et al.* 2007, Salamolard *et al.* 2000, Sodhi & Ehrlich 2010). Predators take prey either opportunistically, i.e., in proportion to their relative abundances, or because of their relative profitability (Mckinnon *et al.* 2013, Quinn & Cresswell 2004, Seaton *et al.* 2008, Tores *et al.* 2005).

Insular environments often determine particular traits in both raptors and their prey populations, characteristic of the so-called "insular syndrome", such as density compensation, wide niche breadth, low breeding rates, high survival, or a lack of migratory behaviour (Carrillo & González-Dávila 2009, Donázar *et al.* 2002; Sanz-Aguilar *et al.* 2015; Thibault *et al.* 1992; Thiollay 1998). Food webs of avian communities in island ecosystems are usually simpler than those in mainland ecosystems (Whittaker & Fernández-Palacios 2007).

In addition, insular top predator populations, such as raptors, are often small, isolated and specialised, making them more prone to extinction than their mainland relatives due to environmental, demographic, stochastic and anthropogenic factors (Bretagnolle *et al.* 2004, Donázar *et al.* 2005, Virani & Watson 1998, White & Kiff 2000).

The diet composition of the Eurasian Sparrowhawk (*Accipiter nisus*) has been well studied throughout continental Europe since it is a common and widespread species and its prey remains (wings, feathers and bones) are easy to collect and identify (Bujoczek & Ciach 2009, Cresswell & Quinn 2004, Götmark & Post 1996, Hernández, 2018, Millon *et al.* 2009, Newton & Marquiss 1982, Opdam 1978, Selås 1993, Solonen 2000, Otterbeck *et al.* 2015). The Eurasian Sparrowhawk has an extreme reversed sexual dimorphism with the female being roughly twice the size of the male (male: 105–196 g, female: 185–350 g, Ferguson-Lees & Christie 2001). It feeds almost exclusively on small and medium-sized birds, rarely exceeding 120 g in body mass, but under particular conditions, it can alternatively consume other prey, such as larger birds, insects, mammals, reptiles and fishes (Barone & Trujillo 1997, Mester & Oliver 2018, Newton 1986, Zawadzka & Zawadzki 2001).

In Madeira and the Canary Islands, an endemic subspecies of Eurasian Sparrowhawk occurs, the Macaronesian Sparrowhawk (*Accipiter nisus granti*), characterized by it slightly smaller size and darker appearance (Ferguson-Lees & Christie 2001, Meyburg *et al.* 2019). Basic knowledge on its biology and ecology is scarce, but it is known that Macaronesian Sparrowhawks are closely associated with forested habitats, both native (laurel forest and Canarian pinewood) and exotic (tree plantations of pines and eucalyptus) for breeding (Delgado *et al.* 1987, Martín & Lorenzo 2001).

Considering the great inter-habitat density variations of potential bird prey communities in the Canary Islands ecosystems (Carrascal & Palomino 2005), diet variations among habitats of this opportunistic predator are expected. In fact, a preliminary study carried out in eleven breeding territories during 1984–1985 indicated slight dietary differences among habitats (Delgado *et al.* 1988).

Understanding how prey densities vary over time or landscape and which prey species contribute the most to the diet are key to the effective conservation of raptor species (Margalida *et al.* 2009, Resano-Mayor *et al.* 2016). In this study, we describe and quantify the spatial and temporal variations of the diet of an endemic insular population of the Macaronesian Sparrowhawk. Specifically, our main aims are: (1) to assess prey selection according to their abundance and body mass, (2) to quantify prey species composition among three insular forest habitats, including both native and exotic, and (3) to make a cautionary comparison of the current diet with that reported in the earlier study (Delgado *et al.* 1988).

2. Material and methods

2.1. Study area and habitats

The Canary Islands are located about 100 km off the Atlantic coast of north-west Africa and are comprised of seven major islands (Fig. 1). The Macaronesian Sparrowhawk breeds on five out of

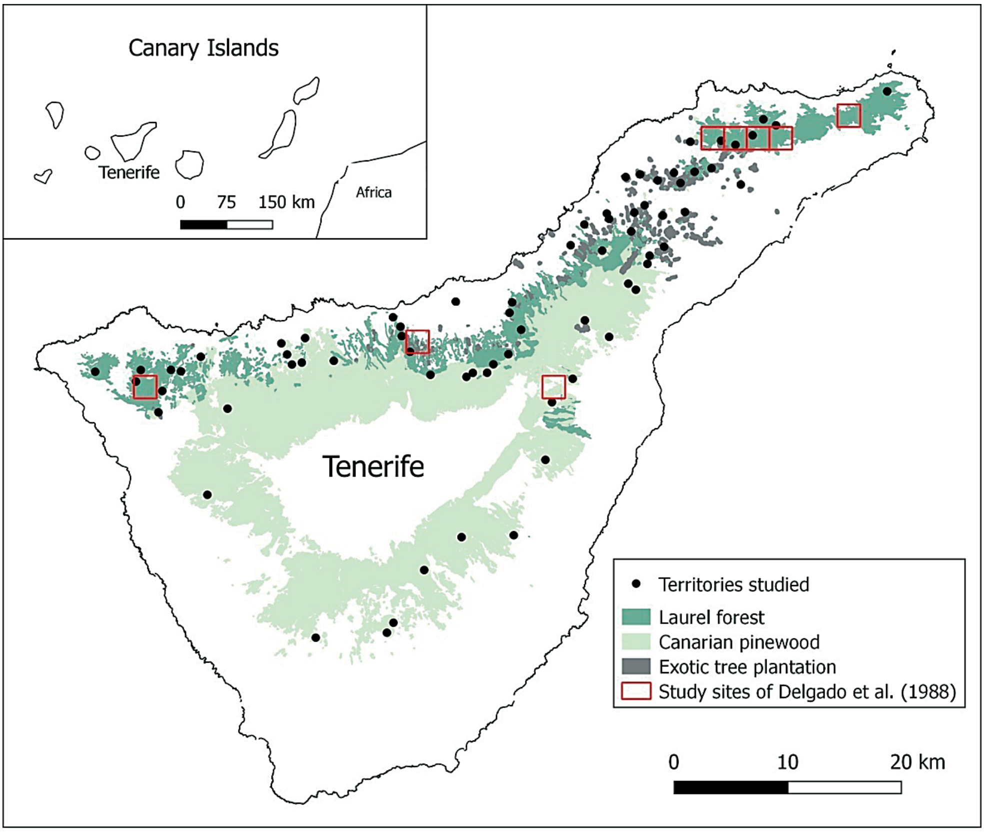

Fig. 1. Distribution of the Macaronesian Sparrowhawk breeding territories studied in Tenerife, Canary Islands, during the 2014–2015 breeding seasons (n = 71). Study sites of Delgado *et al.* (1988) are also highlighted.

the seven islands: El Hierro, La Gomera, La Palma, Gran Canaria, and Tenerife. The study was conducted on Tenerife Island, the largest and highest of the Canaries (2,034 km^2 and 3,718 m a.s.l.). Vegetation and landscape are influenced by humid north-easterly winds, altitude and orientation, ranging from low vegetation on the coasts to different types of forests at altitudes between 350 and 1,900 m a.s.l. (del Arco & Rodríguez 2018). Canarian forests have been intensely exploited by local people during the last five centuries after European colonisation.

The overexploitation led to significant reductions in the original laurel forest and Canarian pinewood at the end of the 19th century (Fernández-Palacios *et al.* 2008, Parsons 1981, Quirantes *et al.* 2011). Throughout the last several decades, intensive forestation campaigns have been carried out mainly with native species to restore the original ecosystems (Parsons 1981, Quirantes *et al.* 2011). The main species used was Canary Pine *Pinus canariensis* (Arévalo & Fernández-Palacios, 2005a), but also other exotic species of *Pinus* spp. and *Eucalyptus* spp. have been planted (Arévalo & Fernández-Palacios 2005b, del Arco & Rodríguez 2018).

To evaluate the diet among habitats we considered three main habitat types: a) the native laurel forest located on north faces at 350–1,300 m a.s.l. and dominated by several species such as *Erica arborea*, *Ilex canariensis*, *Morella faya* and *Laurus novocanariensis*; b) the endemic Canarian pinewood (including all subtypes, i.e., humid, dry, ancient, or plantations) which is a monospecific forest of Canary Pine (*Pinus canariensis*) present at higher elevations than laurel forest (usually >1,300 m a.s.l.); and c) the exotic tree plantations, especially of Monterey pine (*Pinus radiata*), Eucalyptus (*Eucalyptus globulus*) and Monterey cypress (*Cupressus macrocarpa*), established by local authorities during the last few decades in potential areas of laurel forest and Canarian pinewood (del Arco & Rodríguez 2018).

2.2. Determination of diet

As part of a broad study on population status, habitat selection and breeding biology of Sparrowhawks, during March–August of 2014 and 2015, coinciding with its breeding season in the Canaries (Delgado *et al*. 1987), 71 nesting sites and their surroundings distributed around the forested habitat of Tenerife were visited (Fig. 1). One trained and experienced observer identified all prey remains (mainly wing and tail feathers, bones, skulls, bills, legs and hair) found at the typical "plucking posts", or under favourite perches and nests (usually within a 200-m radius of the nests).

Although an intensive search effort (minimum of 15 minutes in each territory) was done, we are aware that some small birds items plucked in the territory could probably be missed due to difficulties in finding their small feathers or scavenger activity of introduced mammals (e.g., *Mus musculus* or *Rattus* spp.). In each visit, the minimum number of prey according to the number of identifiable individual parts was estimated. Mean number of visits per territory was 2.25 ± 1.79 (mean ± SD), ranging from one to 12. All prey remains were thoroughly removed to avoid repetitive counting. Although weather conditions (temperature and humidity) greatly varied across orientation and altitude, storms with heavy rains and/or strong winds are rare during spring and summer (Martín 2001). Therefore, we assumed that detectability of plucked feathers was similar among studied habitats.

In the Canaries, prey remains of Sparrowhawks are easily distinguished from those of other forest predators. Only the Canarian Common Buzzard (*Buteo buteo insularum*) may occasionally consume birds in forested habitats but signs left (feathers or prey remains) and the placement of them are usually different (Brown *et al*. 2003, pers. obs.). Note that the Canarian Common Buzzard is a predominantly cliff-nesting raptor in the Canaries contrary to the typical tree-nesting Common Buzzards from the mainland (Rodríguez *et al*. 2010).

Given the low number of species in avian communities of oceanic islands like that from the Canaries, feathers of most prey can be identified in the field (Petty *et al.* 1995). Thus, only difficult items (especially bones) were collected and identified at the lab. Whenever possible all remains were identified to the species level using personal reference collections of bones and feathers or field guides (Beaman & Madge 1998, Demongin 2016, Jenni & Winkler 1994, Svensson *et al.* 2010).

Prey remains from each habitat (laurel forest, pinewood and exotic tree plantations) were combined to calculate the frequency of occurrence and the relative importance in biomass (%). For birds, mean body mass (g) of prey species were obtained from mean values of individuals captured for ringing on Tenerife (D.P. Padilla and J.C. Illera, *pers. comm.*) or from literature (Delgado *et al.* 1988, Martín *et al.* 2000; Snow & Perrins 1998), averaging values from the two sexes when available. For reptiles and mammals, we used the following values: 15 g for *Gallotia galloti*, 150 g for *Oryctolagus cuniculus*, 110 g for *Rattus* spp. and 20 g for *Mus domesticus* (see SM1).

Nesting territories were classified as belonging to one of the three habitats (laurel forest, Canarian pinewood or exotic tree plantations) according to the highest cover of each habitat type considering a circle of 1.5-km radius centred at the territory (25, 25, and 21 territories in laurel forest, Canarian pinewood and exotic tree plantations, respectively; del Arco *et al.* 2005). Each prey remain was assigned to a nesting territory.

2.3. Diet indicators

Niche breadth and diet diversity were calculated using the standardised Levin's (B_{sta}) and Shannon (*H*') indexes (Krebs 1999) applied to the items consumed. The Levin's index formula is:

$$B = 1 / \Sigma p_i^2 \qquad (1)$$

where p_i is the proportion of each food category consumed. The standardized Levin's index formula is:

$$B_{sta} = \frac{B-1}{B_{max}-1} \tag{2}$$

where B is the Levin's index and B_{max} is the total number of food categories (lowest niche breadth = 0; greatest niche breadth = 1).

The Shannon index formula is:

$$H' = -\Sigma p_i \log p_i \tag{3}$$

where p_i is the proportion of each food category consumed (higher values refer to higher diversity)

Diet overlap between habitats was measured using percentage of food items through Pianka's index (O):

$$O_{jk} = \frac{\sum_{i=1}^{n} p_{ij}\, p_{ik}}{\sqrt{\sum_{i=1}^{n} p_{ij}{}^{2} \sum_{i=1}^{n} p_{ik}{}^{2}}} \tag{4}$$

where p_i is the percentage of prey item i in the diet of habitats/periods j and k (Krebs 1999). Pianka's index varies between 0 (total separation) and 1 (total overlap).

To study avian prey selection among habitats, we used the Ivlev's electivity index (E):

$$E_i = \frac{(p_{ij} - p_{ik})}{(p_{ij} + p_{ik})} \tag{5}$$

where p_{ij} is the percentage of prey item i in the diet and p_{ik} is the percentage of prey density in the wild (Manly *et al.* 2002). Values range from +1 (selection for, or greater accessibility of, a particular prey item) to –1 (avoidance, or inaccessibility of, that item); zero indicates no selection. We used the unique available density (birds/ha) estimates for the vegetation types of Tenerife island, that were obtained in April of 2002 and 2003 by Carrascal and Palomino (2005) conducting linear transects using 25 m band belts at 26 vegetation types. We averaged bird density values for all subtypes of vegetation habitats for laurel forest (named heathlands and laurel forests themselves) and for Canarian pinewoods (dry, humid, ancient, high altitude and young plantations of Canary pine) (Carrascal & Palomino 2005).

For exotic tree plantations, we used mean density values referring to grasslands and cultivated areas, as exotic tree plantations are usually surrounded by these habitats (Carrascal & Palomino 2005, del Arco & Rodríguez 2018). In short, passerines were more abundant in laurel forests and exotic tree plantations respect to the Canarian pinewood, where some non-passerines could be particularly abundant (Carrascal & Palomino 2005). We did not calculate Ivlev's electivity index for exotic, mostly aerial (swifts), or nocturnal (Woodcock *Scolopax rusticola*) avian taxa or those not identified to the species level, as no reliable density values are available. Mammals and lizards were not considered in selection analyses as they constituted a negligible part of the diet.

2.4. Statistical analyses

To test for a potential relationship between prey body mass and selection by Sparrowhawks on prey species, we ran linear models. As a response variable we used the Ivlev's electivity index calculated for all habitats. As explanatory variables we included the body mass of prey and a quadratic term, given the nonlinearity of the relationship (visually checked). We compared two linear models: one with and one without the quadratic term (i.e., Ivlev's electivity index ~ body mass + (body mass)^2 *vs*. Ivlev's electivity index ~ body mass).

To assess the contribution of habitat in the frequency of occurrence of the most frequent prey species, i.e., those species with more than 15 prey items, we used GLMs with a binomial error distribution and logit link. The response variable was a two-column object (number of focal prey / (total number of prey – number of focal prey); all them referred to each territory). We use three explanatory variables: the percentage of land covered by laurel forest, by Canarian pinewood, and by exotic tree plantations.

To evaluate potential long-term temporal changes in the food spectrum, we compared our results to those of the previous study conducted during the 1984–1985 breeding seasons (Delgado *et al.* 1988). This study was based on prey remain analysis but was limited to 11 nesting territories situated on the north face of the island in the laurel forest ($n = 9$), Canarian pinewood (wet) ($n = 1$) and exotic tree plantations ($n = 1$) (Delgado *et al.* 1988). To assess mean differences in the body mass of prey captured in 1984–1985 from those of 2014–2015 and between habitats, we ran a linear model. Body mass was the response variable (log-transformed), while habitat (levels: laurel forest, Canarian pinewood and exotic tree plantations) and study (levels: previous study, i.e., Delgado *et al.* 1988, and this study) were explanatory variables. We also included the interaction habitat × study.

Spatial analysis to classify nesting territories according to the three studied habitats were conducted in Qgis version 3.0.2 (Open Source Geospatial Foundation Project, http://qgis.osgeo.org) and statistical tests were conducted in R (version 3.5.3; R Foundation for Statistical Computing, Vienna, Austria).

3. Results

3.1. General diet composition

A total of 575 prey individuals were identified pooling the three habitats (see SM1). Birds formed the major dietary component of the Sparrowhawk in frequency of occurrence (97.9%) and biomass (98.2%). Some mammals (Rabbit *Oryctolagus cuniculus* and rats *Rattus* sp.) and lizards (*Gallotia galloti*) were rarely consumed (see SM1). A minimum of 26 bird prey species (all native except the Barbary Partridge (*Alectoris barbara*) and the Budgerigar (*Melosipttacus undulatus*) were identified belonging to 12 families, ranging in body mass from the smallest Goldcrest (*Regulus regulus*) (5 g) to the heaviest White-tailed Laurel Pigeon (*Columba junoniae*) (395 g). The most consumed species in numbers were the Atlantic Canary (*Serinus canarius*) (25.7%), the Rock (including Feral and Domestic forms) Pigeon (*Columba livia*) (21.4%), and the Blackbird (*Turdus merula*) (16.3%) (see SM1). Only four species, the Rock Pigeon (47.5%), the Blackbird (13.0%), the Barbary Partridge (10.1%) and the Bolle's Pigeon (*Columba bollii*) (9.7%), accounted for 80.3% of the biomass (see SM1).

The Ivlev's electively index saturated model, i.e., that including the quadratic term, showed an AIC value 4.3 points lower than the AIC of the simple model, i.e., that including only body mass as an explanatory variable. Thus, Ivlev's electively

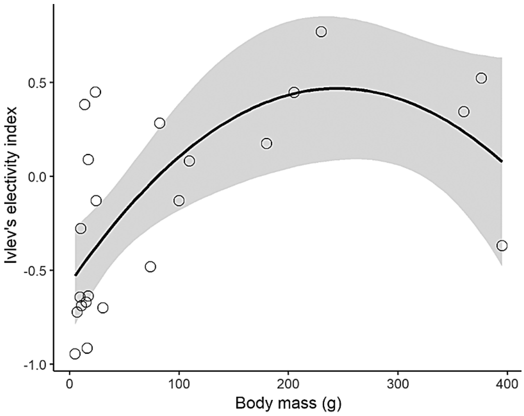

Fig. 2. Relationships between Ivlev's electivity Index and body mass (g) of prey species (circles) of the Macaronesian Sparrowhawk in Tenerife, Canary Islands, during the 2014–2015 breeding seasons.

Table 1. Ivlev's electivity index (*E*) of prey species of the Macaronesian Sparrowhawk on Tenerife, Canary Islands, during the 2014–2015 breeding seasons. See main text for further details on calculation and procedures (species ordered by decreasing body mass). Habitats: 1 = Laurel forest, 2 = Canarian pinewood, 3 = Exotic tree plantation.

Species		Habitats	
	1	2	3
Columba junoniae	–0.36	–1	–1
Alectoris barbara	0.93	0.42	0.5
Columba bollii	0.23	0.51	0.84
Columba livia	0.98	0.95	0.48
Streptopelia decaocto	0.74	0.51	0.33
Falco tinnunculus	–1	0.03	0.69
Streptopelia turtur	–1	–0.01	0.35
Coturnix coturnix	0.86	–1	–1
Turdus merula	0.08	0.39	0.55
Dendrocopos major	–1	–1	0.84
Fringilla teydea	–1	–0.65	–1
Carduelis chloris	0.86	–1	–1
Fringilla coelebs	0.44	0.72	0.31
Motacilla cinerea	0.74	0.72	–0.28
Carduelis cannabina	0.74	0.51	–0.79
Anthus berthelotii	–1	–1	–0.89
Erithacus rubecula	–0.66	–0.66	–0.74
Serinus canarius	0.84	0.46	0.07
Sylvia melanocephala	–1	0.51	–1
Cyanistes teneriffae	–0.33	–0.47	0.42
Sylvia conspicillata	–1	0.51	–1
Phylloscopus canariensis	–0.69	–0.87	–0.73
Regulus regulus	–1	–1	0.84

Table 2. Inter-habitat indicators of avian prey spectrum of the Macaronesian Sparrowhawk in Tenerife, Canary Islands, during the 1984–1985 (Delgado *et al.* 1988) and 2014–2015 breeding seasons.

	Laurel forest	Canarian pinewood	Exotic tree plantations	Total
Period 1984–1985				
Territories studied	9	1	1	11
Sample size	379	68	116	563
Richness	18	10	15	20
Levin's index (B_{sta})	0.31	0.73	0.32	0.31
Shannon index (H')	0.96	0.92	0.91	0.99
Period 2014–2015				
Territories studied	25	25	21	71
Sample size	240	211	112	563
Richness	19	19	15	26
Levin's index (B_{sta})	0.26	0.18	0.27	0.20
Shannon index (H')	0.91	0.85	0.87	0.96

Table 3. Linear model showing the spatio-temporal variations of body mass (g) of avian prey consumed by Macaronesian Sparrowhawk in Tenerife, Canary Islands, during the previous study conducted in 1984–1985 (Delgado *et al.* 1988) and this study (2014–2015). Factors or interactions showing 95% confidence intervals not overlapping with 0 are indicated in bold.

	Estimate	Std. Error	2.5% CI	97.5% CI
(Intercept)	3.729	0.111	3.512	3.946
Previous study	–0.967	0.155	–1.272	–0.663
Laurel forest	–0.087	0.134	–0.351	0.176
Canarian pinewood	0.566	0.137	0.297	0.834
Previous study: Laurel forest	0.454	0.183	0.095	0.813
Previous study: Canarian pinewood	0.139	0.225	–0.304	0.581

index estimated for all habitats was exponentially related to body mass, suggesting that prey around 200–300 g are preferred by Sparrowhawks (Fig. 2, Table 1).

3.2. Inter-habitat diet differences

Considering avian prey, only slight differences in richness and diversity (H') among studied habitats were observed. However, niche breadth (B_{sta}) was clearly lower in the Canarian pinewood than in the other habitats (see Table 2; SM1). Diet overlap, expressed as Pianka's index (O), among native forests (laurel forest and Canarian pinewood) was relatively low ($O = 0.63$). Diet in the exotic plantations was more similar to that in the laurel forest ($O = 0.91$) than that in the Canarian pinewood ($O = 0.87$). Thus, diet in the exotic plantations was more similar to the native habitats than the native habitats were to each other. Species such as the Bolle's Pigeon, the Blackbird, and the Common Chaffinch (*Fringilla coelebs*) appeared in high numbers only in laurel forests. In the Canarian pinewoods, the main counted species was the Rock Pigeon, while in the exotic plantations, the Atlantic Canary and the Rock Pigeon were the most consumed prey (Table 2; SM1). Accordingly, the body mass of prey varied among habitats, being in the Canarian pinewood where Sparrowhawks predated on heavier species (see Fig. 3 and Table 3).

The models indicated that the extension of laurel forest is positively related to the consumption of Blackbird, Common Chaffinch and Bolle's Pigeon, and is negatively related to the consumption of Atlantic Canary and Rock Pigeon. The area covered by pinewood was positively and negatively related to the proportions of Rock Pigeon

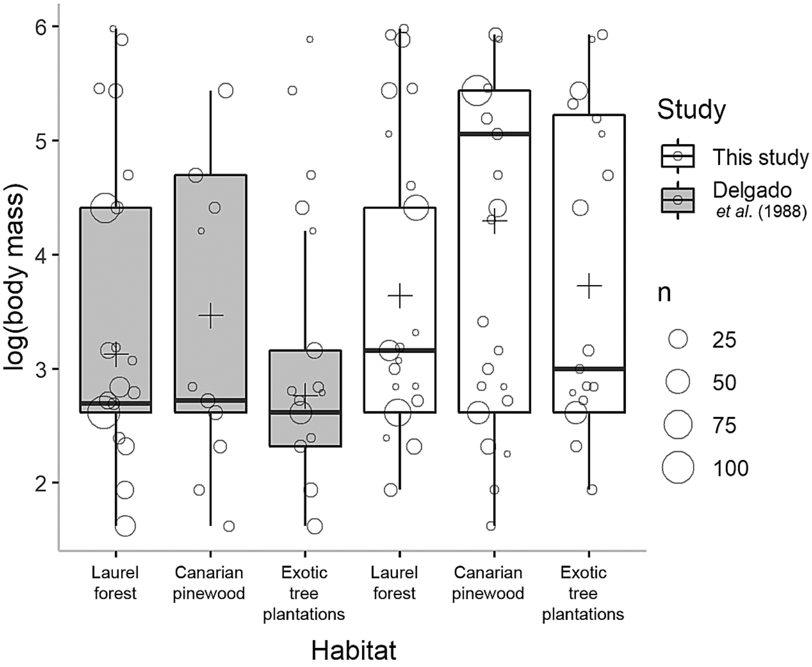

Fig. 3. Box and whisker plots of the body mass (g) of birds consumed by the Macaronesian Sparrowhawk in Tenerife, Canary Islands, according to habitats and studies (Delgado et al. 1988 and this study). The horizontal line within the box indicates the median, the crosses indicate the mean, the boundaries of the box indicate the first and third quartiles, and the whiskers extends to 1.5 times the interquartile range (outliers are not plotted). Open circles are proportional to the number of observations (jittered for better visualization).

and Atlantic Canary, respectively. The area covered by exotic tree plantations was not related to the proportion of any of the most frequent prey, although a negative tendency was observed for Bolle's Pigeon (Fig. 4).

3.3. Temporal diet variation

The diet comparison between 1984–1985 and 2014–2015 revealed some similarities according to Pianka's index ($O = 0.63$), however, some differences emerged in terms of richness, niche breadth and diversity of species composition (see Table 2). During 1984–1985, the House Mouse *Mus musculus* was recorded as the only non-bird prey species, while during the present study we recorded rabbits, rats and lizards (see SM1). Although the number of bird species consumed currently was higher than in 1984–1985 (26 *vs* 20 species), three species recorded in the past were not recorded in the present study (Hoopoe *Upupa epops*, Blackcap *Sylvia atricapilla* and Goldfinch *Carduelis carduelis*). Niche breadth (B_{sta}) and diversity (H') has decreased from 0.31 to 0.20 and from 0.99 to 0.96 respectively (Table 2). A comparison of body mass of the prey consumed in both periods suggest that currently Sparrowhawks predate on heavier species, and the rate of increase has been more pronounced in exotic plantations than in laurel forests (see Fig. 3 and Table 3). In this regard, fourteen avian prey species showed lower numbers now than in the previous study, while the contrary occurred in thirteen species (Fig. 5). Important declines in numbers occurred in small-sized species such as the Goldcrest, the Linnet (*Carduelis cannabina*), the Canarian Chiffchaff (*Phylloscopus canariensis*) and the Robin (*Erithacus rubecula*); while for some relatively large-sized species such as the Rock Pigeon, the Barbary Partridge and the Bolle's Pigeon, their importance in numbers has increased (see Fig. 5).

4. Discussion

4.1. General diet composition

As expected, the diet of the Sparrowhawks in Tenerife is mainly composed of birds ranging from 5 g to almost 400 g (SM1). Studies conducted in European populations, have shown the preference for small-to medium-sized birds (up to 500 g in mass), such as pigeons, thrushes and finches (Bu-

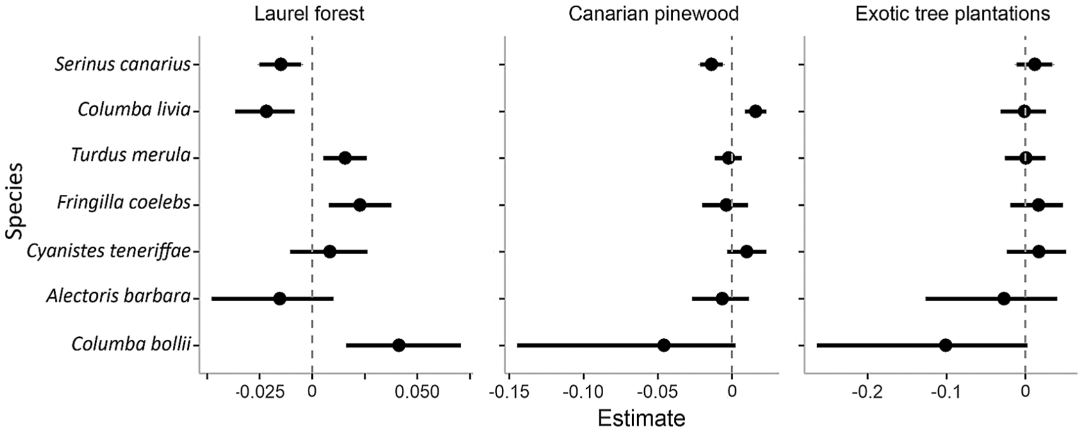

Fig. 4. Estimates (black circles) and 95% confidence intervals (horizontal lines) of the three explanatory variables, i.e., the percentage of land covered by laurel forest, Canarian pinewood, and exotic tree plantations, used in the generalised linear models to explain the proportions of the most frequent prey (> 15 individuals counted) in the diet of the Macaronesian Sparrowhawk.

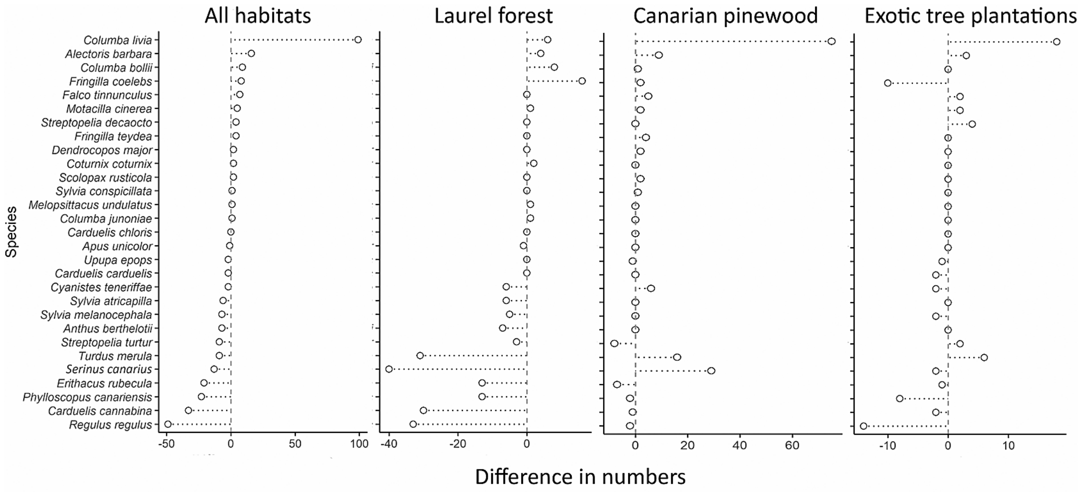

Fig. 5. Difference in the numbers of avian prey species of the Macaronesian Sparrowhawk found in this study minus that found in the previous diet study (Delgado *et al.* 1988). Positive numbers indicate a higher consumption of the focal prey species in the current study.

joczek & Ciach, 2009, Cresswell 1995, Götmark & Post 1996, Hernández 2018, Newton 1986, Opdam 1978, Selås 1993, Zawadzka & Zawadzki 2001).

Several factors, such as size, abundance and foraging behaviour, influence the vulnerability of particular prey species to capture by Sparrowhawks and therefore their importance in the Sparrowhawk diet. In fact, predation risk is high for those medium-sized species (Götmark & Post 1996, Selås 1993) or those that usually forage further away from woody vegetation (Marquiss 2007, Post & Götmark 2006) and are abundant (Petty *et al.* 1995, Zuberogoitia *et al.* 2012). In general, the seven bird species most often consumed by Sparrowhawks in Tenerife fit well within the high predation risk requirements described above as the majority of them usually forage on the ground and they are relatively abundant and widely distributed throughout the island woodlands (Carrascal & Palomino 2005, Martín *et al.* 2000).

Although prey selection is usually strongly influenced by the abundance of the prey species, our results indicated that the diet of the Sparrowhawks in Tenerife does not simply reflect that. In light of the optimal foraging theory there must be a trade-off between abundance (i.e., it may be a more optimal to prefer abundant species including those that are not so profitable), prey body mass (i.e., large preys are the most profitable) and predation risk (i.e., some species-specific behaviour increase catchability) (Cresswell 1995, Götmark & Post 1996, Rytkönen *et al.* 1998, Selås 1993). Thus, medium-sized species could be selected to some degree, so it is intriguing to note that three large-sized species, namely Rock pigeon, Barbary Partridge, and Bolle's pigeon, contributed importantly to the total ingested biomass (SM1).

4.2. Inter-habitat diet variation

Our results indicated variations in the proportions of the prey consumed by Sparrowhawks among the three habitats. Spatiotemporal changes in the food spectrum of a generalist predator such as the Sparrowhawk occur at several scales due to variations in the composition of the prey community. Although to specifically study prey selection (available *vs* consumed prey) independent species richness data from each territory is needed, our approach, i.e., using bird densities in wide habitat types to correlate with consumed prey, constitutes a valuable approach.

Forest habitats show important differences in floristic composition and structure (del Arco & Rodríguez 2018), and consequently, they support well differentiated avian communities (Carrascal & Palomino 2005). Among native habitats, a higher abundance and richness of passerines occur in highly productive laurel forests compared to the usually dryer Canarian pinewoods (Carrascal & Palomino 2005, Delgado *et al.* 2008). Thus, it is not surprising that some of the prey species most consumed by Sparrowhawks in the laurel forests, such as the Blackbird and the Atlantic Canary, reach the highest densities in these complex and diverse habitats within the island ecosystems (Carrascal 1987, Carrascal & Palomino 2005). In contrast, in the Canarian pinewoods (narrow diet niche breadth), Sparrowhawks are forced to predate upon large abundant prey, such as feral Rock Pigeon and Barbary Partridge, because abundance of passerines is low (SM1 and Fig. 3).

In exotic tree plantations, density and richness of birds are usually higher than those of the native forests, especially when they are surrounded by a mosaic of cultivations and pastures (del Arco and Rodríguez, 2018). Many of these plantations have become naturalised spontaneously or due to restoration efforts (Arévalo & Fernández-Palacios 2005a, 2005b, Fernández-Lugo & Arévalo 2009) and are now host to diverse and rich avian communities including many endemic forest-dwelling specialists, e.g. Great-spotted Woodpecker (*Dendrocopos major canariensis*), Bolle's Pigeon or Blue Chaffinch (*Fringilla teydea*) (Lorenzo 2007). Thus, the Sparrowhawk diet in exotic tree plantations is similar to those reported in laurel forests in terms of niche breadth and diversity (Table 2).

4.3. Temporal changes in diet composition

Predation on some species has increased, especially of large-sized birds (Figs. 3 and 5). These temporal differences in diet composition could be partially explained by methodological constraints. First, in the present study we do not account for seasonal variation of the diet spectrum (23% of territories were visited once), so given the Sparrowhawk's sexual size dimorphism and the different male-female roles in reproduction, seasonal differences in diet composition are expected, and consequently in prey sizes (Eldegard *et al.* 2003, Geer 1981, Watts 2014). Second, although sample sizes were similar in both studies, data referred to only eleven breeding territories in the previous study: nine in the laurel forest, one in the Canarian pinewood and one in exotic plantations (Delgado *et al.* 1988). However, 71 territories distributed in the three habitats and scattered throughout the island were sampled in our study. Thus, we cannot rule out observer, seasonal or spatial biases.

Despite these methodological drawbacks, we are confident that at least some of the observed changes in diet composition must be related to changes in prey populations. For example, the abandonment of rural areas together with changes in land uses (Günthert *et al.* 2011, Otto *et al.* 2007) has probably led to a reduction in numbers of some associated birds and thus their importance in the Sparrowhawk's diet. This could be true of the Linnet or the Turtle Dove (*Streptopelia turtur*), the latter perhaps also affected by unsustainable hunting pressure (Lorenzo 2007).

In contrast, anthropogenic activities may be implicated in the increase of some large-sized prey species populations during the last decades and therefore their availability for hunting Sparrowhawks. This is the case of the important expansion of the feral Rock Pigeon in all habitats from sea level to the highest altitudes (*pers. obs.*). The population increase of the Rock Pigeon seems related to increasing food resources from goat farms, reduction in hunting pressure, and recruitment of birds escaped from sport-racing pigeon lofts into the wild population. In fact, 8% (10 out of 123) of predated Rock Pigeons showed racing pigeon rings indicating a captive origin. Another species with increasing populations is the Barbary Partridge, which has benefited from reinforcement programs (i.e., releasing captive origin birds to the wild) conducted by the local insular government for hunting purposes (Emmerson 2004).

In addition, the forest-dwelling specialist endemics, the Bolle's Pigeon and Great-spotted Woodpecker, have benefited from the hunting regulations and the improvement in habitat quality mainly due to restoration or maturation of forests and naturalisation of exotic tree plantations (Lorenzo 2007, Martín *et al.* 2000). Another case to highlight is the addition of the Collared Dove (*Streptopelia decaocto*) to the list of prey consumed by Sparrowhawks. Since its first reliable records in Tenerife at the end of the 1980's (Lorenzo 2007), it has colonised the entire island, both urban and rural areas, and is now a common widespread bird (Palomino & Carrascal 2005).

However, there is no easy explanation for the reduction in small-sized species in the current Sparrowhawk diet, particularly of those considered to have healthy populations such as the Robin, the Canarian Chiffchaff or the Goldcrest (Carrascal & Palomino 2005, Delgado *et al.* 2008, Lorenzo 2007). Under current conditions, i.e., in which it seems that a higher proportion of large birds are available for Sparrowhawks (Rock pigeons, partridges or endemic pigeons), these passerine may be less profitable as they are below the preferred prey size range (Cresswell 1993, Götmark & Post 1996, Hernández 2018, Millon *et al.* 2009, Newton & Moss 1986, Opdam 1978, Selås 1993).

4.4. Conclusions and future studies

Our results indicate that, as an opportunistic predator, the Macaronesian Sparrowhawk has shifted its prey preferences according to prey community composition. Although precise mechanisms regulating these processes are still unknown, some changes observed in prey composition, both spatially and temporally, could be indirectly associated with anthropogenic factors affecting prey numbers. Today in Tenerife, this raptor seems to be a least-concern conservation species, however, its hunting and breeding habitats are still affected by human activities (Arévalo *et al.* 2011, Díaz-Díaz & Loague 2001, Günthert *et al.* 2011, Naranjo 2001) that can lead to negative prey population trends or reduce the availability of suitable breeding sites.

In this scenario, and considering that insular and forest raptor populations are often fragile (Donázar *et al.* 2005, McClure *et al.* 2018), a monitoring program to fully understand the particular predator-prey relationships in the short- and long-term are required to detect possible changes in prey availability. This information could help in the development of effective management actions to guarantee the long-term conservation of this endemic raptor and its related ecosystems.

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Makronesian varpushaukan ravinto luonnonmetsissä ja eksoottisissa viljelymetsissä

Makronesian varpushaukka on kotoperäinen varpushaukan alalaji, jota esiintyy Madeiran ja Kanarian saarten metsissä. Tässä tutkimuksessa selvitettiin sen ravinnonkäytön vaihtelua eri elinympäristöissä Teneriffan saarella vuosina 2014–2015. Vertasimme aineistoa 30 vuoden takaiseen ravintoaineistoon. Selvitimme ravinnonkäyttöä saaliiden jäänteistä kahdessa luonnonmetsäympäristössä (laakeripuumetsä ja Kanarianmäntymetsä) ja viljelymetsissä (vieraslajit).

Varpushaukan ravinto koostui pääosin linnuista (26 tunnistettua lajia, keskimäärin 200–300g), mutta myös pienestä osasta nisäkkäitä ja matelijoita. Kolme lintulajia muodosti 63.4% kaikista saalislajeista (kanarianhemppo *Serinus canarius*, kalliokyyhky *Columba livia* ja mustarastas *Turdus merula*), mutta niiden osuus vaihteli eri habitaateissa.

Ravinnonkäyttö oli monipuolisempaa laakeripuumetsissä ja viljelymetsissä kuin kanarianmäntymetsissä. Verrattuna vuosien 1984–85 aineistoon havaitsimme, että suurikokoisemmat saalislintulajit ovat mahdollisesti yleistyneet, mikä voisi kertoa saalispopulaatioiden muutoksista. Maatalous ja metsänhoito Makronesian varpushaukan habitaateissa voi johtaa sen saaliseläinten vähenemiseen. Tarvitaan lisätutkimuksia selvittämään peto–saalis-vuorovaikutuksia ja kehittämään tehokkaita suojelu- ja hoitotoimenpiteitä, jotka takaavat lajin säilymisen.

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Online supplementary material

Table SM1. Diet spectrum of the Macaronesian Sparrowhawk in the three main forested habitats of Tenerife.