Temporal patterns in prey size between sexes in a raptor with extreme size dimorphism: testing the intersexual competition hypothesis using web-sourced photographs

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DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided at https://github.com/ConnorPanter.

ABSTRACT

In most vertebrates, males are larger than females. For raptors, sexual size dimorphism is reversed, with females being larger. Reversed sexual dimorphism (RSD) in raptors is strongly linked to diet, with species feeding on the most agile prey, for example bird-eating raptors, showing the greatest size differences between the sexes. Hypotheses for reversed sexual dimorphism (RSD) include the 'intersexual competition' hypothesis, which proposes that RSD evolved to enable pairs to expand their dietary niche (taking a wider range of prey sizes) during the nestling period when both sexes occupy and hunt within the same territory, and thereby reduce competition between the sexes. If intersexual competition is responsible for the evolution of RSD, we predict that sex-related differences in prey size and dietary niche breadth will be particularly pronounced during the nestling period (*cf.* the non-nestling period). We explore this prediction in the highly dimorphic Eurasian Sparrowhawk (*Accipiter nisus*), which displays the largest degree of RSD of all raptors, using web-sourced photographs to identify diet throughout the entire year. We analysed 666 photographs of sparrowhawks on their prey over time. In contrast to our predictions, sex-specific prey sizes were most similar during the nestling period compared to any other time of the year. Both males and females reduced the size of their prey during the nestling period which may be a result of the 'ingestion rate' hypothesis, or a strategy employed to prevent hunting-related injuries during this critical period of the year.

KEYWORDS *Accipiter nisus*, citizen science, diet, diet analysis, niche breadth, niche expansion, reversed size dimorphism, sparrowhawk

LAY SUMMARY

- In most animals, males are larger than females.

- For raptors, size differences between the sexes are reversed, with females being largest.
- These size differences are strongly linked to diet, with species that hunt more agile prey (e.g., small birds), showing the greatest sex-related size differences.
- Why do raptors show reversed size dimorphism?
- One theory, the ‘intersexual competition’ hypothesis, suggests that size differences allow both sexes to hunt different sized prey within the same breeding territories – we test this theory on sparrowhawks as they rear chicks in the nest.
- Both sexes reduced their prey sizes and differences between the types of prey were similar during the nestling period and the rest of the year.
- We find no support for the ‘intersexual competition’ hypothesis in sparrowhawks, we believe our findings are because the male reduces the risk of hunting-related injuries while maintaining a high volume of food deliveries into the nest.

INTRODUCTION

In many vertebrates, males are larger than females (Hedrick and Temeles 1989), a trait typically considered to be driven by sexual selection with larger males having a selective advantage when competing for mates (Andersson and Iwasa 1996). In raptors and several other predatory birds, size dimorphisms are reversed with females consistently being the larger sex (Andersson and Norberg 1981, Massemin et al. 2000, Schoenjahn et al. 2020). Although the reason for this reversed size dimorphism (RSD) remains unknown, its degree is strongly linked to diet, with raptors foraging on more agile prey, such as birds, i.e., bird-eating raptors, showing the greatest size differences between the sexes (Newton 1979, Smith 1982, Temeles 1985, Krüger 2005).

Numerous hypotheses have been proposed to explain the evolution of RSD in raptors (Andersson and Norberg 1981, Wheeler and Greenwood 1983, Lundberg 1986, McDonald et al. 2005, Krüger 2005, Pérez-Camacho et al. 2015, 2018, Schoenjahn et al. 2020). Many of these relate to the potential benefit that RSD affords a pair to exploit a wider range of prey sizes during the nestling period, thereby expanding their dietary niche while reducing competition between the sexes within the same breeding territory (Selander 1966, Reynolds 1972, Amadon 1975). This hypothesis is most often termed the 'intersexual competition hypothesis' (Selander 1966) and sometimes the 'niche expansion hypothesis' (Rand 1952). Reducing the competition between the sexes is considered most important during the nestling period when both members of a pair are foraging within the same territory and when food demand from nestlings is greatest (Reynolds 1972, Amadon 1975); allowing both sexes to occupy different subniches. In support of this hypothesis, a recent study found an association between the degree of territoriality and sexual size dimorphism in diurnal raptors (Martínez-Hesterkamp et al. 2018).

Based on the 'intersexual competition' hypothesis, we might predict that prey size differences between the sexes to be most pronounced during the nestling period when both sexes are foraging within the same territory and providing food to their nestlings (Newton 1979). This prediction is based on the pair minimising intersexual competition (Costa et al. 2008) while maximising hunting efficiency (Radford and DuPlessis 2003), during this critical period when food demands from nestlings are greatest (Newton and Marquiss 1982). Thus, the smaller more agile male targets the smaller prey species, when smaller prey such as fledglings are more abundant (Storer 1966, Vedder et al. 2014). The larger less agile female, who also reduces her hunting contributions during the early nestling period (Newton 1986), focuses on the larger prey species and together the pair maximise their hunting efficiency when food demands from nestlings are greatest.

There have, however, been few attempts to test the intersexual competition hypothesis. In part, this may be due to the difficulty of differentiating diet differences in raptors between the sexes and over time. Most methods for studying raptor diet are focused at the nest site during the breeding season, and many approaches are unable to examine differences in diet between the sexes throughout the year; for example, analysis of prey remains at breeding season plucking posts (Selås 1993, Newton 1986, Bujoczek and Ciach 2009) or nest sites (Rytkönen et al. 1998, Huhta et al. 2003, Millon et al. 2009), and/or cameras placed on the nest (Cava et al. 2012, García-Salgado et al. 2015). Recently, a novel approach using web-sourced images has been used to describe both sex- and age-related differences in the diets of two raptor species: the Martial Eagle (*Polemaetus bellicosus*) across Africa (Naude et al. 2019) and the Eurasian Sparrowhawk (*Accipiter nisus* hereafter 'sparrowhawk’) throughout the United Kingdom (Panter and Amar 2021). This method offers the potential to overcome several of the limitations of existing methods used to study raptor diet, specifically enabling sex-specific diet differences to be examined during the full yearly cycle.

In this study we analyse web-sourced images of sparrowhawk on their prey. Our method is unique in that it allows us to analyse sparrowhawk diet over time, which other traditional methods are often unable to achieve. Therefore, we explore diet for both sexes, at monthly intervals, throughout the entire year in the United Kingdom. Sparrowhawk arguably have the highest degree of RSD of any raptor species, with females being almost twice as heavy as males (Newton 1986) and are therefore an ideal model species to explore hypotheses relating to RSD. We examine diet differences between the sexes in relation to: 1) mean prey weights, 2) proportion of different prey size classes and 3) dietary niche breadth, and examine whether these differences shift between the nestling and non-nestling periods, and throughout the year at monthly intervals. Based on the ‘intersexual competition’ hypothesis, we expect that differences in prey weights and prey size classes between the sexes will be most pronounced during the nestling period, with the smaller male hunting smaller prey items and the larger female exploiting the larger prey-sizes. Similarly, we expect that dietary niche breadth will be greatest during the nestling period.

METHODS

Web-sourced data

Photographs of sparrowhawks on prey items within the United Kingdom (UK) were collated between July 24 and August 16, 2019, from various web sources (Panter and Amar 2021). These were then supplemented with further manual searches on Facebook (www.facebook.com), Twitter (www.twitter.com) and BirdGuides (www.birdguides.com) carried out between January 20 and February 8, 2021. We also posted a public appeal via Twitter on February 8, 2021, requesting extra photographs including those specifically taken in May, June and December for which we had the lowest sample sizes (Fig. S1).

For photographs that contained a wild sparrowhawk with its prey, the following data were collected: (1) sparrowhawk age (juvenile < 2cy > adults), (2) sex (male or female), (3) prey species (identified to the lowest taxonomic level possible) and (4) observation date. The ages and sexes of the sparrowhawks were further confirmed by having multiple experienced ornithologists view each photo. For this current analysis only data for adult birds were used. For further methodological details see Panter and Amar (2021).

Prey weight

For each prey item we determined a prey weight (Table S1; Robinson 2005), and allocated the prey to one of three size categories: small (≤ 35g), medium (≥ 36g to ≤120g), or large (≥121g). Some prey were identified as Columbidae spp. but not to species-level, these items were given the average weight of all identified Columbidae items in the diet. We grouped all *Columba livia* (e.g., Rock Doves, Feral Pigeons and White Doves) under the prey item ‘Rock

Dove'. Other prey unidentified to species-level were categorised into one of three size categories: 'Unidentified small bird sp.', Unidentified medium bird sp.' and 'Unidentified large bird sp.'. We calculated mean prey weights for unidentified prey by taking the mean value for all items within each respective size class.

Breeding season for sparrowhawks in the UK

Sparrowhawks are a single brooding species which, in the UK, typically lay between April and May, with an average lay date of May 11 (Robinson 2005). Incubation lasts *c*. 33 days and the nestling period until fledging lasts *c*. 30 days (Robinson 2005). Thus, the earliest chicks would hatch is May, and to be inclusive, in this study we defined May, June and July as the 'nestling period' and the months outside this period as the 'non-nestling period'.

Statistical analysis

All statistical analyses were performed in R version 3.6.3 (R Core Team 2020). We explored differences in prey weight between the sexes across months by fitting a linear model with estimated weight for each prey item as the response variable, and sex, month and their interaction (sex × month) fitted as explanatory variables. We then used a similar model to explore differences in prey weight between the sexes in either the nestling or the non-nestling period. For this analysis, in the initial model we replaced 'month' with 'period' (nestling vs non-nestling). We also explored differences in prey size categories (small, medium and large) between sexes in the nestling and non-nestling period using a multinomial log-linear model implemented with the NNET package (Venables and Ripley 2002), with prey size category fitted as the response variable, and sex, period and their interaction (sex × period) fitted as explanatory variables. Means (± 95% confidence intervals) for each sex in each month and period were generated using the EMMEANS package (Lenth 2019). Lastly, we pooled diet data for both sexes and calculated the Levin's index of niche breadth (*B*) (Levins 1968) to explore if dietary niche differs during the nestling period compared to the rest of the year.

RESULTS

In total, we obtained 666 photographs of adult sparrowhawks on prey items in the UK, with similar numbers for each sex (356 males; 310 females). The mean number of monthly photographs was 26 ± 9 (± SD) for females (range: 10–39) and 30 ± 8 for males (range: 14-42) (Fig. S1).

Prey weights between the sexes differed between the months (sex × month: $F_{1,11} = 2.945$, $P < 0.001$; Table 1). In most months there were large differences in mean prey weights between the sexes, with females generally hunting prey items that were considerably larger than males ($\bar{x} = 300 \pm 169$g vs 118 ± 139g, respectively; ± SD; Table 1, Figure 1). Although marginally non-significant these differences also existed in August and November ($P = 0.052$ and 0.074, respectively; Table 1; Figure 1b). Sex-related differences in prey weights were lowest, and not significantly different between the sexes, during the earlier part of the nestling period in May ($t_{1,642} = 2.365$, $P = 0.773$) and June ($t_{1,642} = 1.026$, $P = 1.000$; Table 1; Fig. 1b).

Changes in prey weights between the sexes differed significantly during the nestling vs the non-nestling period, ($F_{1,1} = 20.743$, $P < 0.001$; Table 1; Figure 1a). While prey weights apparently declined for both sexes during the nestling period (Figure 1b), this change was highly significant for females ($t_{1,662} = -4.235$, $P < 0.001$; Table 1, Figure 1b), but marginally non-significant for males ($t_{1,662} = -2.397$, $P = 0.078$; Table 1; Fig. 1a).

During the nestling period, there was a significant reduction in large sized prey items within the diets of both sexes (females: $t_{1,8} = -3.602$, $P < 0.05$; males: $t_{1,8} = -4.478$, $P < 0.01$; Fig. 1a; Table 2; Table S2); females also increased their selection of medium sized prey during the nestling period ($t_{1,8} = 3.218$, $P < 0.05$; Fig 1a; Table 2; Table S2). For both sexes, dietary niche breath (*B*) was similar between the nestling (*B* = 10.015) and non-nestling (*B* = 10.725) periods (Fig. 2a), suggesting that sparrowhawks do not expand their dietary niche during the nestling period. By month, dietary niche breadth between the sexes was highest in November, December and January (Fig 2b.).

DISCUSSION

In direct contrast to our predictions based on the ‘intersexual competition’ hypothesis, we found that prey size differences between the sexes were lowest during the nestling period, compared to the rest of the year. We also found no evidence that sparrowhawks expand their dietary niche during the nestling period, with similar dietary niche breadth between both the nestling and non-nestling periods.

We predicted that intersexual competition, i.e., differences in mean prey weight, prey size class and dietary niche breadth, would be more pronounced during the nestling period compared to the rest of the year, when both the male and female are hunting within the same smaller breeding territory, energy demands from nestlings are greatest and when reduced competition may offer a selective advantage. In contrast we found the opposite, with the smallest difference in prey size between the sexes occurring during the nestling period, but large significant differences in prey sizes between the sexes outside of the nestling period. This pattern was largely driven by females increasing the proportion of medium sized prey at the expense of larger prey items during this period.

Our findings are further supported by those of Bujoczek and Ciach (2009) who studied sparrowhawks in Poland examining changes in prey sizes during the nesting cycle using prey remains found at the nest. Because of this indirect method, they inferred contribution in terms of prey sizes by the sexes based on the putative behaviours of the sexes at the different breeding stages. As expected, prey sizes were larger during the courtship and nest building period when the females hunt, however, the authors found that prey sizes remained small during nestling and post-fledging periods despite females also expecting to contribute to prey deliveries during this period. Therefore, these findings also suggest that within their study system females are foraging on relatively similar sized prey items to the males during the nestling period.

Because of the difficulties of attributing prey species to sex with existing diet methods, previous studies have used changes in prey size at nest sites to infer behaviour, assuming that the initiation of larger prey items indicate when females are providing food to the nest or to attribute smaller prey items to the male (Selås 1993, Götmark and Post 1996, Bujoczek and Ciach 2009, Millon et al. 2009). Our findings suggest that this could be a flawed approach, since during the nestling period, females appear to shift away from larger items towards small- and medium-sized prey (Geer 1981), which are more similar to the prey of the male. Such a shift therefore can conceal their behaviours (e.g., contributions to provisioning) when inferred only from changes in prey sizes.

Why then do both sexes reduce prey size captured during the nestling period? A possible explanation could be that the provisioning of smaller prey items improves ingestion rates, i.e., ‘the ingestion rate’ hypothesis (Slagsvold and Sonerud 2007), whereby prolonged feeding bouts at the nest are reduced as the male and female (once she returns to hunting during the later stages of the nestling period), hunt smaller prey allowing the pair to quickly return to hunting, maximising hunting efficiency and the amount of food consumed by the nestlings.

Hunting smaller prey may also be a strategy employed to reduce the risk of injury, i.e., there is less risk associated with catching smaller prey items than larger sized prey, during this critical period. Injury during this time to either the male or the female could severely compromise the success of that year’s nesting attempt and given that this species is relatively short lived (Newton 2008), would also compromise their lifetime reproductive success.

Previous studies exploring raptor diets are mostly conducted at the nest site during the breeding season (Selås 1993, Rytkönen et al. 1998, Bujoczek and Ciach 2009, Millon et al. 2009, Lewis et al. 2010, García-Salgado et al. 2015). Other than the combined use of radiotelemetry and activity loggers (Rutz 2003, Rutz et al. 2006) or direct observations (Roth II and Lima 2003, 2006, Millsap et al. 2013), to our knowledge, our method is the only one that offers the ability to both attribute prey captured by the different sexes and to examine prey throughout the year, including both inside and outside of the breeding season. Our method is particularly suitable to study sex-related differences in the diet of species that are sexually dichromatic and dimorphic, allowing the sexes to be readily distinguished from a single photograph (Naude et al. 2019, Panter and Amar 2021). Previous studies have shown that this method can explore sex- and age-related differences in diet, as well as examining diet differences across space (see Naude et al. 2019, Panter and Amar 2021); in this present study we have also now demonstrated the ability to explore temporal (seasonal) differences in diet using this method. This approach has also been used recently to explore and disprove the existence of a diet specialism in a Neotropical *Accipiter* species (Berryman and Kirwan 2021).

However, as with all dietary methods, our approach is not without its limitations. For example, unlike prey remains collected at nest sites, we were unable to identify diet at the pair- or individual-level. Our sample may have also included prey taken by floaters and non-breeding individuals which may have a slight impact on our results. In addition, our method may include a bias towards larger prey items, because larger items may be more obvious to photographers and because sparrowhawks may fly off with smaller prey items and consume them elsewhere, away from areas of human activity (Newton 1979; Panter and Amar 2021).

Despite this, these biases are unlikely to explain the patterns seen in this study, since any such bias is not likely to change during the season, and because smaller prey items increased during the nestling period in our study. This approach, therefore, may allow other ecological hypotheses to be explored which were previously challenging, since it can provide data that were previously not obtainable such as information on diet that can be sex-, age-, region- and time-specific, which most traditional methods have been unable to achieve

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TABLES

Table 1. Mean prey weights for male (*n* = 356) and female (*n* = 310) Eurasian Sparrowhawk (*Accipiter nisus*) throughout the United Kingdom over time. Nestling period = May - July; Non-nestling = August – April. Statistically significant differences in monthly mean prey weight comparisons between the sexes (female – male) calculated from EMMEANs contrasts. CI = confidence intervals. Significant values in bold.

Month	Male		Female		Pairwise comparisons	
	Mean prey weight (g)	95% CI range	Mean prey weight (g)	95% CI range	*t*	*P*
Jan	**118.3**	**(68.6 - 168.0)**	**289.0**	**(221.6 - 356.5)**	**4.000**	**<0.05**
Feb	**157.1**	**(111.7 - 202.5)**	**333.8**	**(286.7 - 380.9)**	**5.306**	**<0.001**
Mar	**156.3**	**(103.5 - 209.1)**	**302.7**	**(252.3 - 353.2)**	**3.937**	**<0.05**
Apr	**125.7**	**(78.6 - 172.8)**	**333.2**	**(275.5 - 390.8)**	**5.472**	**<0.001**
May	99.8	(45.2 - 154.4)	221.3	(136.5 - 306.2)	2.364	0.772
Jun	66.2	(-1.2 - 133.7)	126.2	(33.2 - 219.2)	1.025	0.999
Jul	**79.4**	**(33.5 - 125.3)**	**232.2**	**(178.6 - 285.9)**	**4.247**	**< 0.01**
Aug	144.7	(66.1 - 223.3)	316.4	(267.4 - 365.4)	3.640	0.052
Sep	**107.3**	**(49.6 - 165.0)**	**354.4**	**(303.2 - 405.6)**	**6.293**	**<0.001**
Oct	**129.1**	**(71.4 - 186.7)**	**301.4**	**(245.8 - 356.9)**	**4.224**	**<0.01**
Nov	138.6	(81.0 - 196.3)	283.9	(227.3 - 340.5)	3.530	0.073
Dec	**77.7**	**(22.2 - 133.3)**	**330.6**	**(257.1 - 404.1)**	**5.388**	**< 0.001**
Period						
Nestling	**75.2**	**(37.2 - 113.3)**	**205.7**	**(159.2 - 252.3)**	**4.262**	**<0.001**
Non-nestling	**126.1**	**(109.0 - 143.2)**	**313.3**	**(295.4 - 331.3)**	**14.833**	**<0.001**

Table 2. Differences in the probability of prey size classes (≤ 35g [small], ≥ 36g to ≤120g [medium] and ≥121g [large]) in the diet of male (*n* = 356) and female (*n* = 310) Eurasian Sparrowhawk (*Accipiter nisus*) throughout the United Kingdom, comparisons between the nestling (May – July) and non-nestling (August – April) periods. Statistically significant differences in prey size classes between the sexes (female – male) calculated from EMMEANs. CI = confidence intervals. Significant values in bold.

Period	Prey size class	Male		Female		Pairwise comparisons	
		Probability	95% CI range	Probability	95% CI range	*t*	*P*
Nestling	**Small**	**0.55**	**(0.43 - 0.67)**	**0.05**	**(0.02 - 0.09)**	**-6.811**	**<0.001**
	Medium	0.33	(0.21 - 0.44)	0.33	(0.18 - 0.48)	0.013	0.999
	Large	**0.12**	**(0.04 - 0.20)**	**0.58**	**(0.42 - 0.73)**	**5.896**	**<0.01**
Non-nestling	**Small**	**0.39**	**(0.32 - 0.46)**	**0.05**	**(0.02 - 0.09)**	**-10.157**	**<0.001**
	Medium	**0.28**	**(0.22 - 0.35)**	**0.11**	**(0.06 - 0.15)**	**-5.221**	**<0.01**
	Large	**0.33**	**(0.26 - 0.39)**	**0.84**	**(0.78 - 0.89)**	**13.912**	**<0.001**

FIGURES

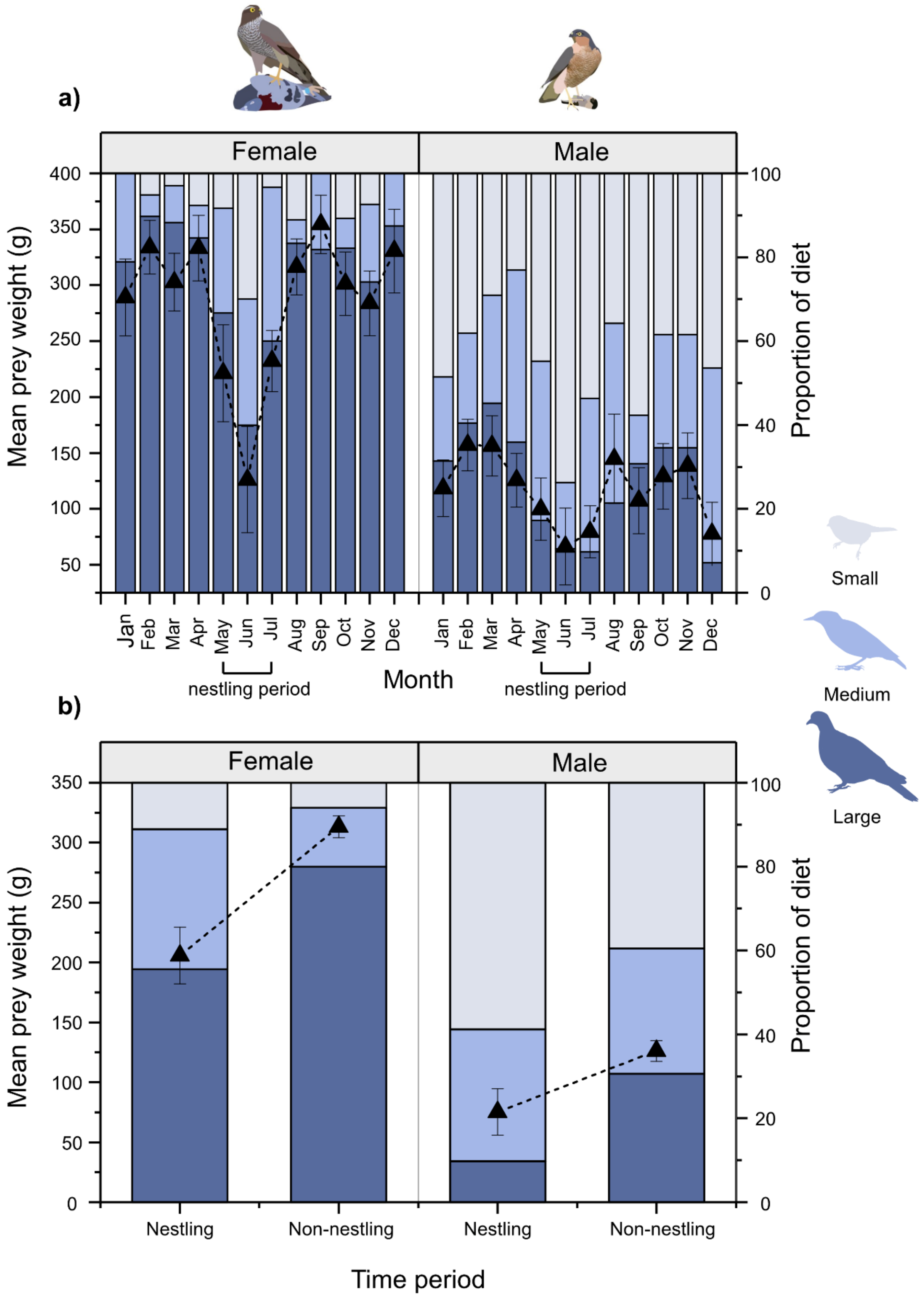

Figure 1. Mean prey weights and proportion of different prey size classes (small, medium and large) within the diet of male and female Eurasian Sparrowhawk (*Accipiter nisus*) by a)

throughout the year at monthly intervals and b) period (Nestling = May – July; Non-nestling = August – April). Error bars = standard error.

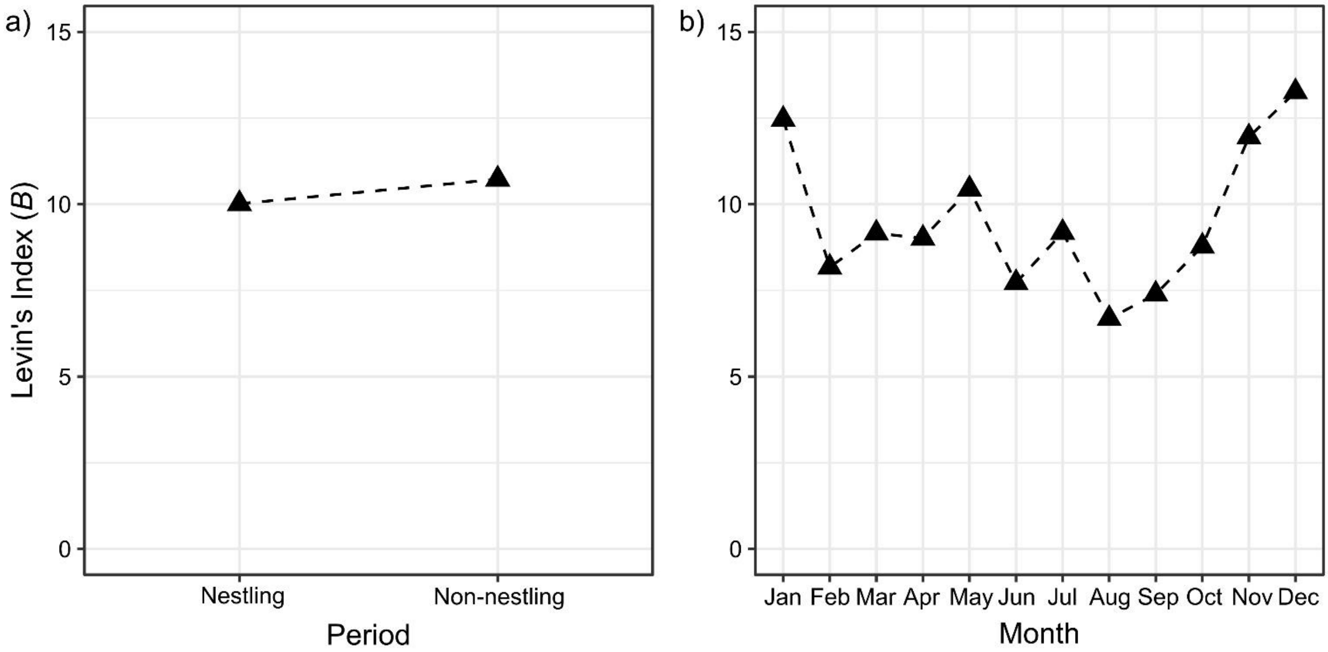

Figure 2. Levin's index of niche breadth (*B*) in the diet of Eurasian Sparrowhawk (*Accipiter nisus*) throughout the United Kingdom between a) the nestling and non-nestling periods and b) throughout the year at monthly intervals. Nestling period = May – July; Non-nestling = August – April.

FIGURE CAPTIONS

Figure 1. Mean prey weights and proportion of different prey size classes (small, medium and large) within the diet of male and female Eurasian Sparrowhawk (*Accipiter nisus*) by a) throughout the year at monthly intervals and b) period (Nestling = May – July; Non-nestling = August – April). Error bars = standard error.

Figure 2. Levin’s index of niche breadth (*B*) in the diet of Eurasian Sparrowhawk (*Accipiter nisus*) throughout the United Kingdom between a) the nestling and non-nestling periods and b) throughout the year at monthly intervals. Nestling period = May – July; Non-nestling = August – April.

GRAPHICAL ABSTRACT