Naturwissenschaften (2007) 94:1015–1020
DOI 10.1007/s00114-007-0284-5

SHORT COMMUNICATION

Male-biased predation of western green lizards by Eurasian kestrels

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Received: 9 July 2006 / Revised: 30 May 2007 / Accepted: 25 June 2007 / Published online: 19 July 2007

Abstract Selective predation can be an important force driving the evolution of organisms. In particular, sex-biased predation is expected to have implications for sexual selection, sex allocation and population dynamics. In this study, we analysed sex differences in the predation of the western green lizard (*Lacerta bilineata*) by the Eurasian kestrel (*Falco tinnunculus*) during the reproductive season. In addition, we investigated whether the rate of predation differed during the 8-year study period and among the three habitats studied. We collected lizard remains from nest boxes of kestrels. Freshly killed lizards were sexed by visual inspection, whilst the sex of head remains was assigned by analysing the cephalic scale morphology using geometric morphometrics. Our results show that the risk of being predated by a kestrel in our population was overall about 3.55 times higher for males than for females. To our knowledge this is the first study showing a male-biased predation in a lizard species. The selective predation of males was consistent between years over the 8-year study period (1999–2006) and also consistent between the three types of kestrel hunting habitat. Overall predation rates on lizards differed between habitats, depending on the year. We propose that the observed sex-biased predation is mainly due to sex differences in lizard behaviour.

Keywords *Falco tinnunculus* · Geometric morphometrics · *Lacerta bilineata* · Prey selection · Sex-biased predation

Introduction

Selective predation may be considered a major force acting on the evolution of organisms. More specifically, the effects of prey selection have been recognized mainly in the subsequent trade-off found between sexual selection (i.e. differential mating success) and natural selection (i.e. chances of survival; Lima and Dill 1990).

Several studies have tried to identify which elements make prey more vulnerable to avian predators (Mueller 1968, 1971; Smallwood 1989). Most of these studies have evaluated the role of three characteristics of the prey (activity pattern, colour and body size) with respect to the selection made by avian predators. Prey mobility has been proposed to be the most important factor in determining predation by avian predators (Smallwood 1989). However, prey selection mediated by visual cues is likely to be the result of the combination of behavioural traits and of the colour pattern of the prey (Forsman and Appelqvist 1998).

Sex-related differences in behaviour and phenotype may determine a sex-specific risk of predation, which is usually higher in males (Magnhagen 1991; Christe et al. 2006). During the mating season, males are particularly active in searching for a mate and are consequently more likely to be detected by predators. For example, the acoustic signals emitted by male frogs increase their risk of being predated (Ryan 1985). Males of many bird species have bright colours and perform conspicuous displays that are designed to attract mates, but that may attract predators as well (e.g. Korpimäki 1985; see also Götmark 1992).

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In a study using artificial models of male and female sand lizards (*Lacerta agilis*), both sexes were equally selected by avian predators although the male models were characterised by a more marked nuptial colouration (Olsson 1993). In another study using plastic models of male specimens of two Australian rock dragon lizards (*Ctenophorus decresii* and *C. vadnappa*), a higher predation risk was measured for brighter males (Stuart-Fox et al. 2003). However, in the latter study, no between-sex comparisons were made.

In addition to conspicuous colouration, body size may also be an important factor determining differential predation on lizards. Such size-based predation on lizards is not necessarily unidirectional. For example, American kestrels (*Falco sparvierus*) preferably preyed on large *Anolis* lizards (McLaughlin and Roughgarden 1989), whilst kookaburras (*Dacelo novaeguineae*) mainly preyed on small and medium-sized skinks, *Eulamprus tympanum* (Blomberg and Shine 2000).

In this study, we investigate if there is a sex-biased predation of western green lizards (*Lacerta bilineata*) by Eurasian kestrels (*Falco tinnunculus*) during the reproductive season over an 8-year period. In addition, we examined whether the rate of predation differed throughout years or with respect to hunting habitats.

Materials and methods

Sample collection

The study was carried out in central Italy, in the area surrounding Rome, over a period of eight breeding seasons (May–June, from 1999 to 2006). Overall, 225 remains of western green lizards were collected from 69 nest-boxes (3.3 specimens per nest-box; range, 1–18) of kestrels, located in three main habitat types: (1) cereal and cultivated fields, (2) set asides and pasturelands, (3) fields with bushes and woody patches (see Costantini et al. 2005).

Some nest-boxes appear in our data-set more than 1 year (mean ± s.d., 1.62±0.97). This is because there are some nest-boxes in which reptiles were consistently preferred to other prey, year after year (Costantini et al. 2005). Therefore, in the light of the renowned fidelity of kestrels to their nest (Village 1990; personal observation), some pairs are likely to have contributed to our sample for multiple years. To avoid such pseudoreplication, the nest-box was included in the analyses as a random factor. This allowed us to check for the effect of individuals specialized in the predation of lizards.

Of the 225 specimens sampled, 134 freshly killed lizards were sexed by visual detection of the presence of hemepenes, whilst 91 specimens were collected as head remains and the sex was assigned according to the morphological criteria described below.

Sex determination

The sex determination of the 91 heads was performed using geometric morphometrics (Bookstein 1991; Marcus et al. 1996), through Procrustes superimposition, Principal Components Analysis (PCA) of the Partial Warps and Discriminant Analysis (see Zelditch et al. 2004 for details on the multivariate approach to landmark data). A two-dimensional configuration of 16 landmarks was used to describe the pattern of the cephalic scales of 20 males and 20 females (Bruner et al. 2005). Landmarks represented the boundaries of the frontal, fronto-parietal, parietal, inter-parietal and occipital scales (Fig. 1a). No differences in the PCA components and patterns were found by confronting unilateral vs bilateral configurations, or by countering simmetrised vs original data.

Coordinates were sampled from photographs in dorsal view by using *tpsDig 1.20* (Rohlf 1998a). Procrustes Superimposition and PCA were computed using *tpsRelw 1.18* (Rohlf 1998b), whilst the centroid size (index of size; square root of the sum of squared distances of a set of landmarks from their centroid; Marcus et al. 1996) was computed by *tpsRegr 1.20* (Rohlf 1998c).

The morphospace computed from the PCA of all shape variables (partial warps) is polarised by the first component (30% of the variance), which is largely related to the head size differences (loading=0.75). The next four components explained 18, 11, 9 and 8% of the remaining differences, respectively. The discrimination analysis was limited to the first five components because (1) this allows us to maintain a sufficient statistical robustness considering the balance between number of variables and sample size, (2) the sixth component explains less than 5% of the variance and this estimate is considered scarcely reliable in morphometric studies, (3) the first five PCs explained a large proportion of the variance (76%).

For the same reasons, the discrimination was not computed using the residuals directly after superimposition.

The discriminant vector (Fig. 1b) was able to correctly classify 85% of the specimens a posteriori (males 17/20; females 17/20), assuming a 50% probability of representation for each sex. Using the centroid size as the discriminant variable, 90% of the specimens were correctly classified a posteriori (males 19/20; females 17/20). Principal components and centroid size were not used together to avoid introducing redundancy related to the allometric component and PC1.

Results

One-hundred males and 34 females were identified within the freshly killed group of specimens. Eighty-five percent (n=77) of the 91 undetermined specimens was classified as

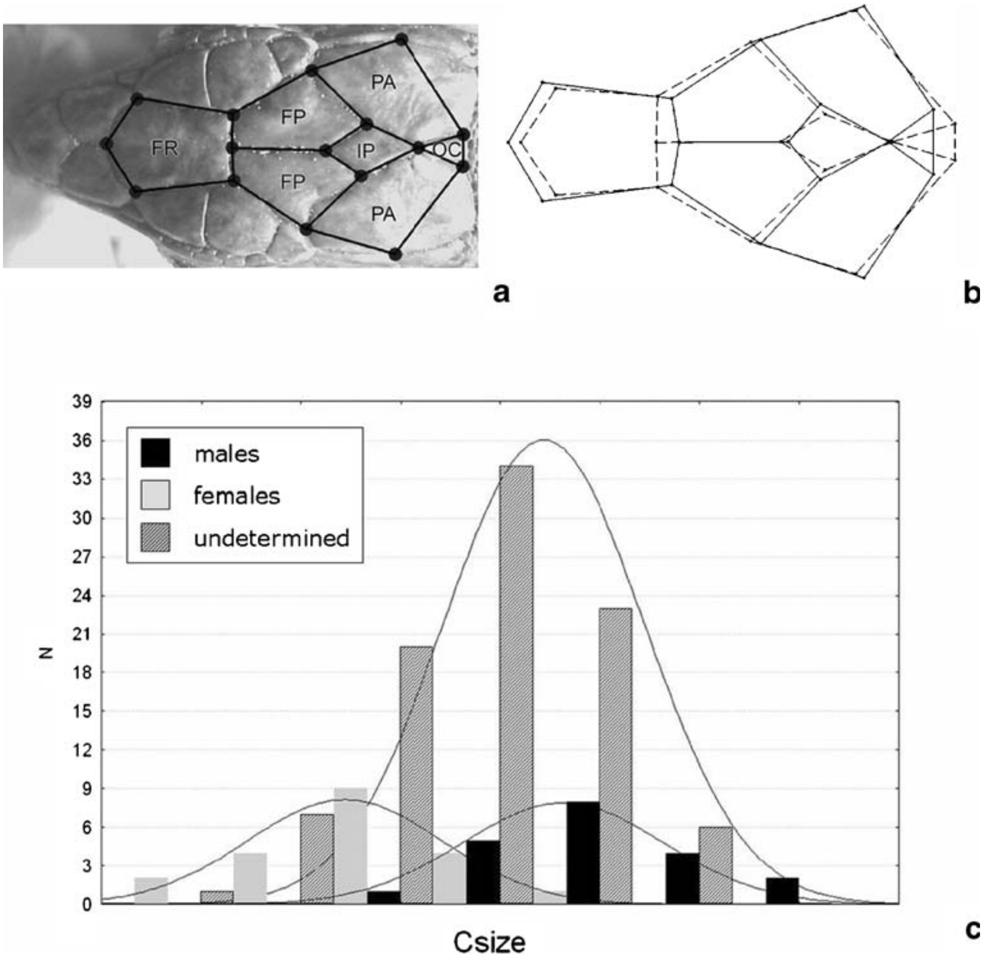


Fig. 1 **a** Configuration of landmarks and dorsal view of the cephalic scales. Scales are labelled (*FR* frontal; *FP* frontoparietal; *IP* interparietal; *PA* parietal; *OC* occipital). **b** The linked configurations show the head morphology variation along the discriminant vector (male: *dashed line*; female: *solid line*). **c** Comparison of the distribution of centroid size between a sample of reference (20 males and 20 females) and a sample of 91 undetermined specimens preyed by kestrels whose sex was determined by head morphology

male by using the shape components only, whilst 81% (n=74) was classified as male by using the centroid size (mean number of the two results: males, 75.5; females, 15.5). The distribution of prey head size (larger in males) was skewed toward higher values and it matched the distribution of males (Fig. 1c).

Overall, our data show that males suffered higher predation than females, with 78% (calculated on the mean numbers) of all the specimens collected being composed of males ($\chi^2=69.4$, $df=1$, $P<0.001$). The higher predation on males persisted in similar proportions during both months of sampling (contingency table: $\chi^2=0.8$, $df=1$, $P=0.38$). A three-factor mixed analysis of variance (nest-box as random factor; sex, year and hunting habitat as fixed factors) with Satterthwaite's approximation of degrees of freedom (Table 1) showed that (1) the predation differed between habitats depending on the year (habitat × year: $P=0.014$; Fig. 2), (2) males were more abundant than females in the diet ($P<0.001$) and (3) the male-biased predation was constant across years (sex × year: $P=0.65$) and habitats (sex × habitat: $P=0.38$).

Table 1 Outcome of a three-factor mixed analysis of variance (nest-box as random factor; sex, year and hunting habitat as fixed factors) with Satterthwaite's approximation of degrees of freedom (*df*)

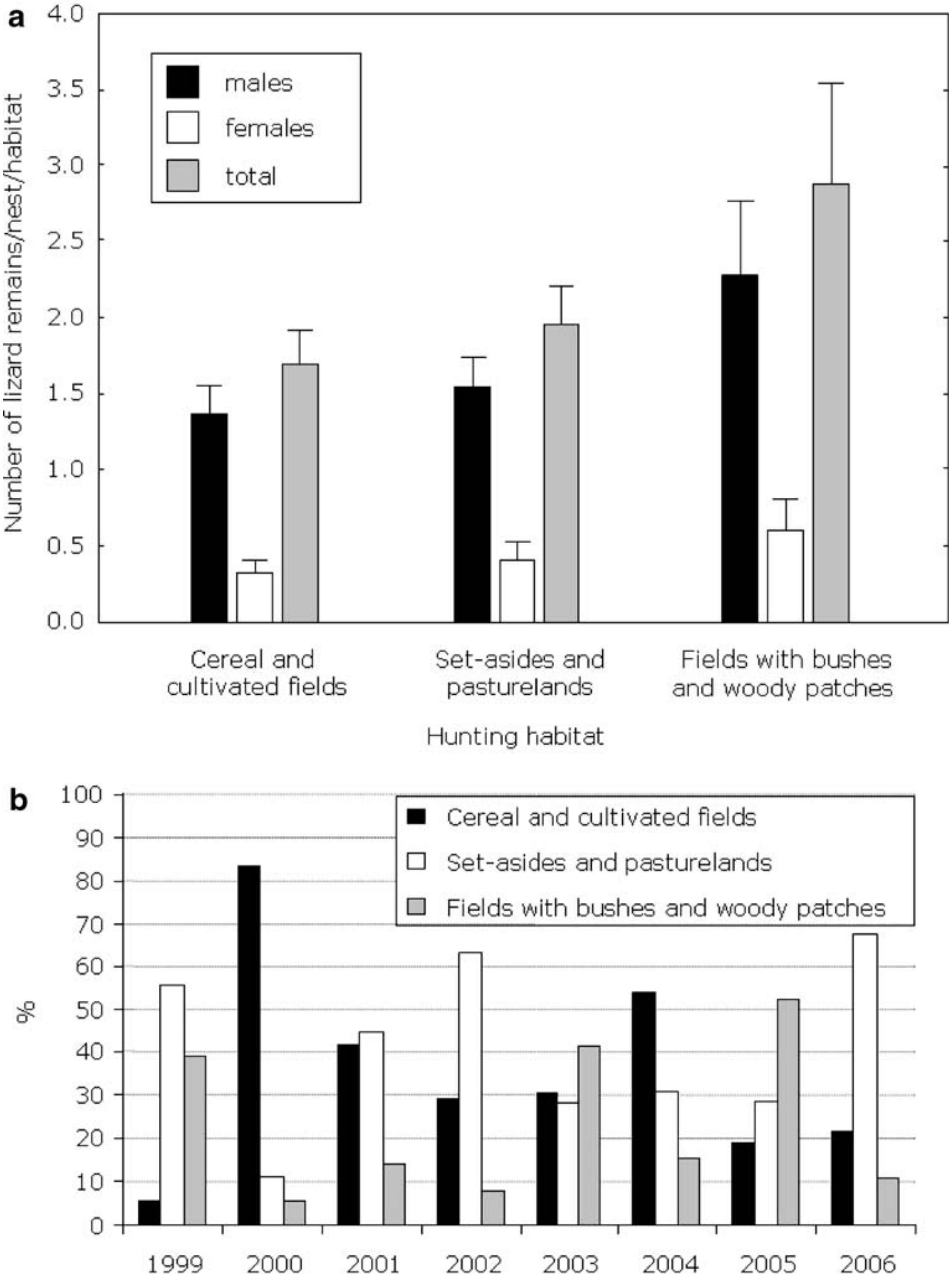
	F	*df*	*P*
Habitat	4.25	2,14.93	**0.035**
Year	1.37	7,97.81	0.227
Sex	61.64	1,39	**<0.001**
Habitat × year	2.44	14,39	**0.014**
Habitat × sex	1.00	2,39	0.378
Year × sex	0.72	7,39	0.653

Significant results are shown in bold type.

Discussion

Results of this study suggest that predation of western green lizards by Eurasian kestrels is male-biased, as evidenced by geometric morphometric analyses of head remains and as well as visual sexing of freshly killed specimens collected from nest boxes over 8 years. To our knowledge, this is the first study showing male-biased predation in a lizard species. Sex ratios of lacertid populations are usually recorded to be around 1:1 or slightly skewed toward one sex (reviewed in Turner 1977). A 1:1 sex ratio in France (Saint Girons et al. 1989)

Fig. 2 **a** Number of lizard remains collected from each nest in the three main hunting habitats of kestrels occurring in our study area (central Italy, Rome province). Values are shown as mean±s.e.m. **b** The predation rate on western green lizards differed between habitats, depending on the year. In 2005, predation was particularly higher in fields with bushes and woody patches (Tukey test for unequal sample sizes: $P<0.01$)



has been reported for the western green lizard. In addition, an unbiased sex ratio seems to occur in our study area (our own capture data: 6 males and 15 females; M. Capula, personal communication). Thus, the sex ratio of the prey we observed is too skewed to reflect the sex ratio in the population. Assuming a 1:1 sex ratio in the lizard population we studied, the overall risk of male lizards of being predated was 3.55 higher than in females.

These findings show that male green lizards are exposed to a greater risk of predation by kestrels than females during the reproductive season. The effect of prey size on avian predation was not falsified as shown by the skewed distribution toward larger specimens (see Fig. 1c). However, our findings do not allow us to determine whether the size was the main cause driving selective predation on males or a correlate of other factors (e.g. behaviour). It is likely that larger lizards might be preferred by raptors to smaller ones (Martín and López 1996). As male green lizards are just slightly larger than females, the size could be just a secondary correlate of other sex-related characteristics rather than the main explanatory factor.

Lizards are characterized by different sex-related behaviours during the reproductive season. These include different patterns of mobility, refuge use and territorial defence that are likely to lead to a different vulnerability to avian predation (Perry and Garland 2002; Martín et al. 2003). For example, male lizards adjust the length of time spent inside a refuge to both the risk of predation and the reproductive cost of refuge use (i.e. loss of mating opportunities), whilst females mainly adjust it to predator avoidance alone (Martín et al. 2003). Moreover, male lizards have larger home ranges than females (Perry and Garland 2002). As a consequence, higher predation on male lizards could be due to their higher activity level in open areas. Indeed, it has been hypothesised that lizards might be particularly easy to detect by raptors when moving in open areas regardless of differences in body size or colour (Olsson 1993; Castilla and Labra 1998). However, our own data do not allow us to draw general conclusions about the cues kestrels use to prey on male lizards.

The type-II functional response is a common model of predator–prey interaction and is well documented in empirical studies (Abrams 1990; Sonerud 1992). The form of a type-II functional response expects predators to consume their prey at a rate which increases proportionally as prey density increases. The rate of avian predation should therefore be expected to increase as a consequence of an increase in the abundance of lizards. Green lizards inhabit bushes and patches with dense vegetation along pastures and fallow fields, riverbanks and edges of woods (Arnold and Burton 1978). Our results actually show that the number of green lizards in the diet of kestrels was higher in areas with bushes and woody patches. However, such habitat-dependent pattern does not seem to be a general rule as it varied from one year to another. This suggests that the abundance of green lizards in the diet of kestrels could also depend on the feeding habits of the raptors themselves (Costantini et al. 2005) or on the availability of alternative prey in the same habitats.

Sex-biased predation may be expected to have some effect at the population level. For example, selective predation on male agile frogs (*Rana dalmatina*) by European polecats (*Mustela putorius*) has been found to decrease the occurrence of polyandry by affecting sex ratio, male abundance and sexual behaviour (Lodé et al. 2004).

A recent study reported that an excess of males in common lizard (*Lacerta vivipara*) populations influences aggressive behaviour toward adult females which leads to population decline (Le-Galliard et al. 2005). If this holds also for our green lizard population, the skewed predation towards males could avoid detrimental effects on population stability.

Conclusions

Our study showed that male western green lizards suffered higher predation by kestrels than females. We propose that such sex-biased predation is mainly related to sex-based differences in behaviour in the lizard. However, future studies should test this hypothesis specifically. Moreover, it would be interesting to evaluate the effects that such a sex-biased predation might have on population viability and, in particular, on the potential consequences for small and large populations, taking into account the concept of reproductive value and the types of mating system, i.e. monogamous vs polygamous.

Acknowledgements We thank the editor and three anonymous reviewers for their valuable comments that substantially improved the manuscript. The association *Ornis italica* sponsored part of the field work. ENEL and ACEA provided logistic support for the monitoring of the nest boxes on their utility lines. The geometric morphometric analysis was performed at the Human Paleontology Laboratory of the University *La Sapienza*, directed by Giorgio Manzi. David Costantini was supported by a PhD Fellowship from the University *La Sapienza*. The study is in accordance with the current Italian law.

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