

Assessment of nestling diet and provisioning rate by two methods in the Lesser Kestrel *Falco naumanni*

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Abstract. Nowadays the use of remote photography systems is very popular for diet assessment. Despite the popularity, there is a greater need for evaluation of these systems against traditional methods of diet assessment, such as direct visual observation. The diet of Lesser Kestrel nestlings and adult provisioning rate were assessed using cameras and direct observations at four nests with various brood sizes during the breeding season in 2013. The study was conducted in an intensively cultivated area that belongs to a Special Protected Area of the Natura 2000 network in central Greece. Diet composition (prey type and size) was not affected by the recording method, the sex of adults, the brood size, the period of the day or the age of nestlings. Tettigoniidae was the most frequent prey delivered by adults. Our results from both methods showed that males delivered more prey items than females, supporting the general consensus of reversed sexual dimorphism for the Lesser Kestrel. The provisioning rate was not significantly related to brood size, but it was affected by the method of observation, parent sex and the interaction of method and nestling age. According to the direct observations, provisioning rates increased as nestlings grew up, while they decreased based on camera information. Higher provisioning rates recorded in direct observations at later nestling stages, can be explained by higher food requirements of nestlings. The decrease in provisioning rate with nestling age was mostly affected by the camera function, as a result of digital limitations, nest type and Lesser Kestrels behavior.

Key words: prey provisioning pattern, diet assessment, remote photography method, Lesser Kestrel, *Falco naumanni*, food, feeding

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INTRODUCTION

Studies on food habits are essential for understanding the feeding ecology of predators and thus for the management and conservation of predator populations (Marti et al. 2007, Bakaloudis 2009, 2010). Diet studies of raptors provide information on prey provisioning rate, prey size, prey species (Margalida et al. 2009, López-López & Urios 2010, Bakaloudis & Vlachos 2011) as well as information on the distribution, abundance, behavior and vulnerability of the prey (Bakaloudis et al. 1998, Bontzorlos et al. 2005, Rodríguez et al. 2010). The diet of a species may differ between sexes and different age stages with significant effects on its populations (Newton 1998). Different provisioning rates in raptors may also be associated with Reversed Sexual Size Dimorphism

(RSD), which is explained by ecological, behavioral and/or role-differentiation traits (Newton 1979, Margalida & Bertran 2000, Margalida et al. 2007b). In the case of raptor species with reversed sexual size dimorphism, differences observed between species in foraging ecology, parental roles, and demands imposed by egg production are associated with the degree of sexual size dimorphism (Andersson 1994, Margalida & Bertran 2000, Margalida et al. 2007b). In some species, especially in hawks and falcons, the female is twice the weight of the male. In most species, after offspring hatch, males are responsible for hunting while females deal with the care of nestlings (Newton 1979, Eldegard et al. 2003). The ratio of RSD determines the extent of female participation in hunting (Krüger 2005). Males are smaller than females, possibly in order to supply

frequent meals to the nest and to reduce the required food of the pair (Newton 1979, Massemin et al. 2000, Krüger 2005). There is less of a need for the female to dismember prey, and consequently when feeding on small prey she can dedicate more time to other parental activities. Studies using video monitoring for different species of raptors have shown that the extended relegation of females to sedentary offspring food processing leaves greater potential for differential selection on male and female body size (Sonerud et al. 2014). In addition, provisioning rate of parents varies in response to brood size. In some raptors, males tend to increase their provisioning rate as brood size increases (e.g. Kestrel *Falco tinnunculus* — Tolonen & Korpimäki 1994, American Kestrel *Falco sparverius* — Dawson & Bortolotti 2003), whilst in others, this occurs for females (e.g. Sparrowhawk *Accipiter nisus* — Newton 1986, Hen Harrier *Circus cyaneus* — Leckie et al. 2008).

Among *Falco* species encountered in Europe, the Lesser Kestrel *Falco naumanni* is less dimorphic, with the female being 24% heavier than male (Negro et al. 1992). Males also play an important role during the breeding season. While feeding the female during the period of courtship and early brooding period, the male also shares the incubation of eggs and carries the majority of food to nestlings (Donazar et al. 1992). In contrast to other more dimorphic raptors, female Lesser Kestrels hunt from the onset of egg hatching, but to a lesser extent than the males, because females are primarily responsible for chicks brooding (Andersson 1994).

The Lesser Kestrel is a colonial falcon, recently qualified as “least concern” in Europe (BirdLife International 2016). Nevertheless, considerable declines locally still occur: the Greek population, which comprises c. 15% of the European total, has been declining and it is mostly concentrated in Thessaly (Vlachos et al. 2004a). In Greece Lesser Kestrels start laying from late April to early May (authors’ own data). It is a central place forager species (Tella et al. 1998, Franco & Sutherland 2004, García et al. 2006), feeding mainly on arthropods and occasionally on small mammals (Vlachos et al. 2003, Rodríguez et al. 2010), which locate in intensively cultivated areas, grasslands and field margins (Vlachos et al. 2004b, 2015, Goutner et al. 2015).

There is a variety of methods assessing food habits of raptors and each shows advantages, disadvantages and biases (Marti et al. 2007). Indirect methods, such as pellet or prey remains analysis,

have the disadvantage of underestimating the daily rate of transferred prey and imprecise nestling diet assessment. Direct methods, as visual observations and cameras, were considered better and less biased for evaluating food habits (Marti et al. 2007) and especially for the evaluation of nestling dietary habits (Bakaloudis & Vlachos 2011). Most researchers evaluated these methods through the comparison between direct and indirect methods (Real 1996, Redpath et al. 2001, Margalida et al. 2007a, Selås et al. 2007, Sánchez et al. 2008, Bakaloudis et al. 2012). Other studies evaluated the biases between different direct (Margalida et al. 2005, Rogers et al. 2005) or indirect methods (Graham et al. 1995, Oro & Tella 1995). The difficulties and problems of each method may vary and when cameras are used there is a need for comparison with other methods (Margalida et al. 2005, García-Salgado et al. 2015, Francksen et al. 2016). Both, the high quantity of data obtained in given time of effort and the reappraisal of delivery pictures are referred as the two advantages by using camera in studies of prey delivery in raptors (Margalida et al. 2005).

Although, similar studies on other raptors have already been published, there is a lack for the Lesser Kestrel, because it is difficult to use direct methods due to its particular nesting requirements. Also, its prey provisioning rate for the nestling period has not been studied. The primary aim of this study was to evaluate two direct methods of food habit assessment. Therefore, we investigated the prey provisioning rate and the diet composition (prey species and sizes) of the Lesser Kestrel using direct visual observations and camera observation. Within this context, we tested the following predictions concerning the provisioning rate: a) the average food provisioning rate is expected to be similar between the two methods, b) the average food provisioning rate of male is expected to be higher than that of female, and c) nests containing large broods (5 nestlings) is expected to show higher provisioning rates than nests containing smaller broods (3 nestlings). We also examined the influence of the recording method, the sex of adults, the brood size and the age of nestling on diet composition.

MATERIALS AND METHODS

Study area

The study area is situated in the eastern part of the Larisa plain in Thessaly, central Greece. It includes

a colony of c. 120 pairs, which breed in nest boxes mounted on trees of a pine grove, near the village of Armenio (22°41'39"E, 39°29'07"N). The main habitat types in the area are cereals, cotton, orchards and natural grasslands. The region belongs to the Special Protection Areas (GR1420011, Periochi Thessalikou Kampou) of the Natura 2000 network and it is an important breeding area of the Greek Lesser Kestrel population. The climate is thermo-Mediterranean, with mild rainy winter, dry and hot summer and a mean annual precipitation of about 465 mm (Vlachos et al. 2015).

Field procedures and data collection

The diet of Lesser Kestrel nestlings was determined during the nestling season of 2013, using two methods: a) by placing cameras, and b) by direct observations at four nests. The selected nest boxes were located in neighboring trees and had the same orientation.

When clutch was completed, we selected two nests with 3 eggs and two nests with 5 eggs to establish a WSCA02 — BirdCam 2.0 w/ Flash infrared-triggered camera. In nests where eggs did not hatch, nestlings of the same age were transferred to complete the initial brood size. The acceptance of nestlings from adoptive parents has been reported in Lesser Kestrels (Donázar et al. 1991, Tella et al. 1997). All transferred nestlings to host nests successfully fledged. So nestling translocation is a feasible technique for researchers studying Lesser Kestrels. Cameras were tested in order to select the more suitable settings. Motion at the entrance of the nest triggered the cameras and 1 to 10 images per trigger were taken with a delay of one minute for the camera to be ready for a new shot. Appropriate settings were installed before using the cameras and images were stored in 4 GB memory cards. In order to achieve higher efficiency and better recognition of the prey, cameras were placed at a distance of approximately 60 cm from the nest box entrance. Also, some external modifications were made by placing a wooden platform in front of the entrance of every nest box in order to prevent adults entering the nest at high speed. Nests were visited weekly from the middle of the incubation period and cameras were recording for two days per visit. Images were taken between 07:00 and 20:00 whenever the camera was triggered by the activity of a Lesser Kestrel in the nest. For each parent that arrived at the nest, sex, arrival time, presence of food, prey type and size of prey were recorded.

To compare the methods, the same four nests that were mounted with cameras were simultaneously directly observed from a distance of c. 50 m with the use of 20 × 50 binoculars. The data obtained among the four nests were similar. On each visit, sessions of direct observations were randomly distributed over the three periods of day (morning: 07:00–11:59, noon: 12:00–16:59 and afternoon: 17:00–20:00), while the respective cameras were in operation. Similar recording protocols were used for both methods. A total of 516 observation-hours were conducted during the nestling period. When direct observations were not conducted, camera recordings were omitted from the analyses. So, 516 recording-hours and 2,713 images were analyzed during the nestling period. No prey deliveries were recorded by both methods during the incubation period.

For both methods, prey items delivered to nests were identified and classified into one of eight prey types: 1) Acrididae (grasshoppers and locusts), 2) Tettigoniidae (bush-crickets), 3) *Gryllotalpa gryllotalpa* (European mole cricket), 4) unidentified Orthoptera, 5) Coleoptera (beetles), 6) unidentified insects, 7) Chilopoda (centipedes), and 8) Arvicolinae (voles). In addition, the prey items were arbitrarily assigned to six prey size groups, according to Lesser Kestrel's bill length (BL): 1 = one BL, 2 = two BLs, 3 = three BLs, 4 = four BLs, 5 = five BLs, and 6: > five BLs.

Statistical analysis

We built generalized linear mixed-effect models (GLMM) with multinomial distribution and the generalized logit link function. Prey type and prey size were used as the response variables, while the recording 'method' (direct observation/cameras), the 'sex' (male/female) of adults, the 'brood size' (3 nestlings/5 nestlings), the 'period' (morning/noon/afternoon) and all the two-way interactions were the explanatory variables. The 'age of nestling' was included in the models as a covariate.

We performed a linear mixed effect model (LMM) to investigate which factors influence the food provisioning rate (Steen et al. 2011, 2012). Prey provisioning rate was used as the response variable and was expressed as the number of prey items delivered to the nest per hour. The variables inserted into the model were 'method' (direct observations/cameras), 'sex' (male/female), 'brood size' (3 nestlings/5 nestlings), 'period' (morning/noon/afternoon), 'nestling age' and all two-way interactions as explanatory variables.

The response variable was square root transformed according to Freeman & Tukey (1950) to obtain normality of the residuals. The best model was selected according to the statistical concept of model selection, using the Maximum Likelihood estimation method.

The effects of explanatory variables in both procedures were investigated by stepwise-deletion (Murtaugh 2009). We built a maximal model with all explanatory variables and removed the least significant terms one at a time until only significant terms ($p < 0.05$) were included in the model.

Nest ID was inserted as random effect (Subject) to control for any inter-pair variation in prey capture and allocation (Sonerud et al. 2013).

All statistical analyses were conducted using the statistical package IBM-SPSS Statistics version 23. The level of significance for all tests was set as 0.05.

RESULTS

Prey frequencies reported by the two methods

Insects and Chilopoda were recognized by both direct observations ($n = 595$) and cameras ($n = 103$), whereas small mammals were only recorded by cameras and Coleoptera only by direct observations (Table 1).

Prey types and prey size groups

Prey types that delivered to the nests were not significantly affected by any of the explanatory variables introduced in the model ($p > 0.05$). Method, sex, brood size, period, nestling age and all two-way interactions made no contribution to the model. The final fitted model included only the method, but was not significant ($F_{7,684} = 0.821$, $p = 0.570$).

A total of 564 prey items were sized in direct observations, while only 75 were sized with cameras. Prey size groups delivered were not

Table 1. Frequency of occurrence (%F) of prey species delivered by adult Lesser Kestrels at nests, studied with direct observations and cameras. Sample sizes are in parentheses.

	%F	
	direct observations (n = 595)	cameras (n = 103)
Orthoptera		
Acrididae	6.05	0.97
Tettigoniidae	83.36	79.61
<i>Gryllotalpa gryllotalpa</i>	0.67	3.88
unidentified	0	6.80
Coleoptera	1.51	0
unidentified insects	5.04	1.94
Chilopoda	3.36	5.83
Mammals		
Arvicolinae	0	0.97

influenced by method, sex, brood size, period, nestling age and all two-way interactions. The best model generated by stepwise deletion showed that brood size was not significant ($F_{5,629} = 0.875$, $p = 0.498$).

Food provisioning

The overall mean (\pm SE) food provisioning rate calculated from direct observations was 1.13 ± 0.07 prey items/hour (95% CIs: 0.98–1.28) while cameras recorded 0.19 ± 0.03 prey items/hour (95% CIs: 0.12–0.26). The mean food provisioning rate was significantly affected by method ($F_{1,235.989} = 15.059$, $p < 0.001$), sex ($F_{1,235.989} = 11.237$, $p = 0.001$) and method \times nestling age interaction ($F_{2,237.079} = 10.745$, $p < 0.001$) (Table 2). Direct observations showed significantly higher provisioning rate than cameras ($t = 3.881$, $df = 235.989$, $p < 0.001$), and significantly less females delivering prey than males ($t = -3.352$, $df = 235.989$, $p = 0.001$) (Fig. 1). The mean food provisioning rate recorded by direct observations increased ($t = 3.728$, $df = 237.203$, $p < 0.001$) as nestlings became older, while the respective provisioning rate recorded by cameras decreased ($t = -2.701$, $df = 237.203$, $p = 0.007$).

Table 2. Output of LMM investigating the factors affecting the food provisioning rate of adult Lesser Kestrels. Parameter coefficients (Estimate and Standard Error (S.E.)) of the best model are presented in the Freeman & Tukey (1950) square root scale. Nest ID included as random effect to control for possible variation caused by individual differences.

Parameters	Estimate	S.E.	df	t	p-value
Intercept	1.665464	0.135625	16.884	12.280	< 0.001
Method: direct observations	0.534336	0.137697	235.989	3.881	< 0.001
Sex: female	-0.250435	0.074709	235.989	-3.352	0.001
Method (direct observations)*age	0.018728	0.005023	237.203	3.728	< 0.001
Method (camera)*age	-0.013569	0.005023	237.203	-2.701	0.007

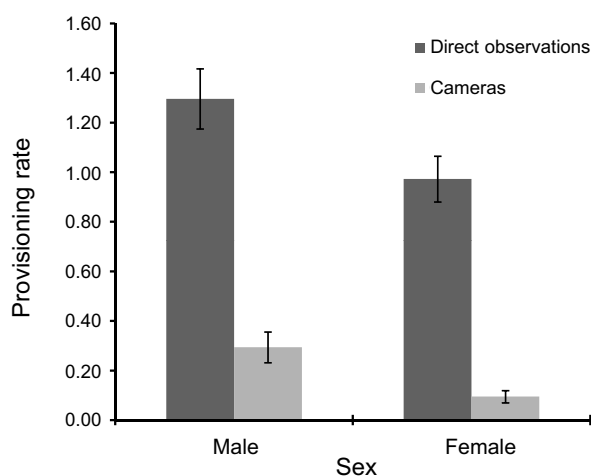


Fig. 1. Mean food provisioning rate (prey items/hour \pm S.E.) of male and female Lesser Kestrels by the methods of direct observations and cameras.

DISCUSSION

Diet composition and method evaluation

The investigation of the delivered food to Lesser Kestrel nestlings using two direct methods reinforced the existing knowledge of the dominance of insects in the species' diet (Negro et al. 1997, Rodriguez et al. 2010). A total of seven prey types were identified by the camera method, including small mammals which are part of the species diet (Vlachos et al. 2003), in comparison to the six prey types identified in direct visual observations. Despite this, our results showed that both methods are efficient in prey species recognition. In contrast to cameras, direct observations recorded prey delivery rates approximately six times higher. There are some possible reasons for the camera's failure to record all prey deliveries. The equipment used to our study belongs to infrared-triggered cameras. This equipment is activated by an object (i.e. animal) moving in the field of the camera (Swann et al. 2004). These passive systems are not triggered by weather or vegetation though false activations may have occurred. Additionally, in some cases the sensor is not activated (Swann et al. 2011). Another explanation is that artificial nests (nest-boxes) are likely to be a disadvantage to the cameras' activity due to the limited exposure of adults delivering food at nest, which may be out of the cameras field of view. A better system for monitoring raptors breeding in nest-boxes use video motion detection is described by Steen (2009), this method has been systematically tested and captured every prey delivery. Direct visual

observations also showed that the rate of prey delivery was positively related to nestling age. As nestlings grow, their food requirements become higher leading to an increased parent food provisioning activity at the nests (Bakaloudis & Vlachos 2011). This process can be so fast that the sensor of camera cannot be activated to catch the adults with the delivered prey. In our study, a high proportion of images taken by cameras showed parents that entered the nest or remained in the field of camera after they had delivered the prey to the nestlings. Franzreb & Hanula (1995) faced the same problem during the study of a hole-nesting bird, the Red-cockaded Woodpecker *Picoides borealis*. In some cases, the photos showed the adults merely remaining in the camera field after having delivered the prey to nestlings. External modifications of nest-boxes prevent birds from flying directly into the nest (Currie et al. 1996) so prey recording is more efficient. However, even these modifications cannot prevent photographing problems. All Orthoptera that were recorded by direct observations were identified and classified in family groups. On the other hand, Lesser Kestrels tended to obstruct the view of the Orthoptera prey so that the prey was only partially visible, making accurate identification difficult. Some Orthoptera insects were impossible to identify into family groups with camera footage, and thus were classified as "unidentified". Most studies, where cameras were used for evaluating the food habits of a species, were conducted at natural nests open from the top (Rogers et al. 2005, Tornberg & Reif 2007, García-Salgado et al. 2015, Francksen et al. 2016). This open nest structure provides a larger field of view and exposes the prey for longer time on camera. Other researchers used video settings on cameras in order to cover a wider range of activities (Delaney et al. 1998, Dykstra et al. 2002, Margalida et al. 2006, Grivas et al. 2009), but even video settings cannot replace an observer. In our study, we observed a kleptoparasitic behavior of a female in neighboring nests, which is also reported by Negro et al. (1992) in Lesser Kestrels. With digital equipment it is difficult or impossible to record such behaviors.

Role of sex and brood size on provisioning rate

Our findings support our second hypothesis, that male Lesser Kestrels have higher provisioning rates than females. The life history of raptors involves distinct roles between the two sexes. Lesser Kestrel is more likely to follow the provisioning standard proposed by Newton (1979).

Although the species shows low RSD (Negro et al. 1992), our results showed asymmetric parental roles in prey provisioning, as observed in other moderately dimorphic raptors (Margalida et al. 2007b). Male undertake the majority of hunting, while the female brood the nestlings and hunts on a smaller scale. It has been argued that the need for aerial agility for hunting in males and the accumulation of nutrients for egg production and parental care in females could explain the sexual division of parental activities (Andersson & Norberg 1981). Lesser Kestrels hunt insects which are small-sized prey. Our results showed that both sexes delivered similar prey species of equal sizes. Insect prey handling and processing to nestlings is not a time consuming activity. This insectivorous diet allowed the females to be able to hunt from the onset of egg hatching. As the nestlings are getting older, they can handle the prey more easily so the female is devoted to hunting (Sonerud et al. 2014).

Our results showed that prey provisioning rate was independent of the number of nestlings. Also, prey type and size was not related to the number of nestlings. This response indicates that Lesser Kestrels probably do not adjust their parental effort according to brood size as observed in other raptors (Tolonen & Korpimäki 1996, Dawson & Bortolotti 2003, Zuberogitia et al. 2013). This investment strategy suggests that parents may deliver more food in larger broods within the limits of parental work (Drent & Daan 1980). If the number of nestlings exceeds these limits, the parents are unable to respond accordingly and the cost of brooding may cause survival problems on adults (Winkler 1987). Lesser Kestrels normally lay 3–5 eggs so they can adjust their parental investment in broods as large as 5 nestlings. Therefore, our results suggest that males deliver the majority of food independent of brood size. On the other hand, females are also responsible for brooding, and their provisioning rate seems to be independent of brood size. Our hypothesis that larger broods induce higher food provisioning rates than small broods was not supported.

The present study indicated that the specific camera model performed poorly for this purpose and is less suited for monitoring prey deliveries at raptor nests. Both methods indicated that certain prey species had relatively high participation in Lesser Kestrel's diet. For the rational management of the species, a continuous monitoring of food habits should be established. In future studies, density estimates of prey species should be

included. Continuous monitoring would reveal aspects of the foraging ecology of the species that was out of the scope of this study and uncover possible responses to the fluctuations of various prey species populations.

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STRESZCZENIE

[Określanie diety oraz częstości karmienia piskląt u pustuleczki za pomocą dwóch metod bezpośrednich]

Najpopularniejszymi obecnie metodami określania składu pokarmu dostarczanego pisklątom przez ptaki dorosłe jest, uruchamiany zdalnie lub automatycznie, system rejestrowania obrazu. Popularność tych metod wiąże się z potrzebą oceny jakości uzyskiwanych danych względem metod stosowanych wcześniej, takich jak bezpośrednia obserwacja lub analiza resztek pokarmowych znajdujących w gniazdach.

Skład pokarmu piskląt pustuleczki oraz częstość przynoszenia pokarmu przez ptaki dorosłe określano za pomocą kamer uruchamianych przez fotokomórkę działającą na ruch umieszczonych przy gniazdach i bezpośrednich obserwacji w czterech (tych samych) gniazdach o dwóch wielkościach lęgów (3 i 5 piskląt). Badania przeprowadzono w 2013 r., na terenie należącym do sieci Natura 2000 w środkowej Grecji.

Pasikoniki Tettigonidae były najczęstszą zdobyczą przyniesioną do gniazda przez ptaki dorosłe (Tab. 1). Przyniesienie drobnych ssaków zostało zarejestrowane wyłącznie na obrazach z kamer, zaś chrząszczy – tylko podczas obserwacji bezpośrednich (Tab. 1). Stwierdzono, że na skład pokarmu piskląt, zarówno jego rodzaju, jak i wielkości, nie wpływała metoda pozyskania danych (z kamer lub obserwacji), płeć ptaków dorosłych przynoszących pokarm, wielkość lęgu, pora dnia ani wiek piskląt (Tab. 2).

Wyniki uzyskane obiema metodami wykazały, że samce dostarczały więcej ofiar niż samice (Fig. 1). Częstość przynoszenia pokarmu nie była istotnie związana z liczbą piskląt, ale była zależna od metody obserwacji, płci rodzica oraz interakcji między metodą zbioru danych a wiekiem piskląt. Bezpośrednie obserwacje wykazały, że częstość przynoszenia pokarmu wzrastała wraz z wiekiem piskląt, natomiast dane zebrane przy pomocy kamer — że spadała. Częstsze karmienia rejestrowane podczas bezpośrednich obserwacji można wyjaśnić wyższymi wymaganiami pokarmowymi rosnących piskląt. Natomiast zmniejszenie częstości przynoszenia pokarmu wraz z wiekiem potomstwa zarejestrowane za pomocą kamer wynika z ograniczeń związanych z funkcjami samej kamery, rodzaju gniazda oraz zachowania pustuleczek.