Delivery of Common Lizards (*Zootoca* (*Lacerta*) *vivipara*) to nests of Eurasian Kestrels (*Falco tinnunculus*) determined by solar height and ambient temperature

Ronny Steen, Line M. Løw, and Geir A. Sonerud

Abstract: Recent development in video monitoring has allowed collecting of data on prey deliveries at raptor nests, and this offers an opportunity to relate prey selection to short-term changes in environmental factors on a scale of hours. Whereas raptors may specialize on ectothermic prey at southern latitudes, only some generalist raptors may include such prey in their diet at northern latitudes. In particular, at northern latitudes the activity pattern of ectothermic reptiles is strongly dependent on the prevailing weather conditions. To test whether this dependence affects the exposure of reptiles to raptors, we used video recording of prey deliveries at nests of the Eurasian Kestrel (*Falco tinnunculus* L., 1758) at 61°N in Norway, where the Common Lizard (*Zootoca* (*Lacerta*) *vivipara* (Jacquin, 1787)) is the only lizard available to kestrels. The probability that a prey item delivered at a kestrel nest was a lizard increased towards midday and also increased independently with increasing ambient temperature, which on average, was 20.2 °C when lizards were delivered compared with 15.7 °C when other types of prey were delivered. Thus, the delivery of lizards by kestrels in our study may be regarded as a functional response, where the abundance of lizards is determined by solar height and ambient temperature.

Résumé : Des progrès récents en surveillance vidéo permettent la récolte de données sur l'approvisionnement des proies dans les nids de rapaces, ce qui donne l'occasion de mettre en relation la sélection des proies et les changements à court terme dans les facteurs de l'environnement à l'échelle des heures. Alors que certains rapaces peuvent se spécialiser pour les proies ectothermes aux latitudes du sud, seuls quelques rapaces généralistes peuvent inclure de telles proies dans leur régime aux latitudes nordiques. En particulier, aux latitudes nordiques, les patrons d'activité des reptiles ectothermes dépendent fortement des conditions climatiques courantes. Afin de vérifier si cette dépendance affecte l'exposition des reptiles aux rapaces, nous utilisons des enregistrements vidéo d'approvisionnements de proies dans des nids de faucons crécerelles (*Falco tinnunculus* L., 1758) à 61°N en Norvège, où le lézard commun (*Zootoca* (*Lacerta*) *vivipara* (Jacquin, 1787)) est le seul lézard disponible aux crécerelles. La probabilité qu'une proie livrée aux nids de crécerelles soit un lézard augmente vers le milieu de la journée et elle augmente aussi de façon indépendante lorsque la température ambiante s'éleve; cette température est en moyenne de 20,2 °C lors de la livraison des lézards, par rapport à 15,7 °C lors de la livraison des autres types de proies. Ainsi, la livraison de lézards par les crécerelles dans notre étude peut être considérée comme une réponse fonctionnelle, dans laquelle l'abondance des lézards est fonction de la hauteur du soleil et de la température ambiante.

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Introduction

How short-term changes in environmental conditions on the scale of hours affect prey selection by birds in general, and raptors in particular, is poorly known. Traditionally, the diet of raptors has been estimated from prey remnants and regurgitated pellets collected at or near the nest during or after breeding, or from prey stored in the nest. This has restricted analyses of environmental effects to an interannual scale, as typical for studies of effects on diet of changes in prey abundance (e.g., Korpimäki 1988; Reif et al. 2001; Millon et al. 2009). Collecting such data repeatedly during the breeding period has allowed relating diet change to environmental change on a shorter intra-annual scale, for instance during snow melt (e.g., Sonerud 1986). Further refinement in temporal resolution has traditionally required direct observations of prey deliveries from a blind near the nest, but this is very time consuming and has therefore rarely been used (e.g., Suomus 1952; Sulkava 1964; Stinson 1980; Newton 1986 and references therein; Redpath 1992). Moreover, the opportunity offered by such observations to relate prey type to environmental factors on a detailed temporal scale of hours has almost never been realised (for an exception see Stinson 1980), in contrast to what is the case for foraging behavior per se (e.g., Machmer and Ydenberg 1990). Recently, the development of various video techniques for recording prey deliveries at raptor nests (Steen

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R. Steen,[1] L.M. Løw, and G.A. Sonerud. Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway.

[1] Corresponding author (e-mail: ronny.steen@umb.no).

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2009 and references therein) has allowed a cost-efficient collection of prey delivery data with temporally high resolution (e.g., Grønnesby and Nygård 2000; Selås et al. 2007; Tornberg and Reif 2007). Still, to the best of our knowledge, such data have hitherto not been used to relate changes in prey selection to corresponding short-term changes in environmental factors.

Raptors breeding at southern latitudes often prey upon ectothermic prey, and some to such an extent that they are classified as insect eaters or reptile eaters (Newton 1979). At northern latitudes, where reptiles and large insects are less abundant, generalist raptors may include such prey in their diet (e.g., GilDelgado et al. 1995; Selås 2001), but the mechanisms determining this inclusion is poorly known. Reptiles may minimize the risk of being preyed upon by staying hidden but will face increased mortality when they have to leave the refuge for foraging or other activities (Lima and Dill 1990; Caro 2005). For ectothermic reptiles such as lizards, external heat is required for maintaining an optimal body temperature to maximize physiological functions (cf. Avery et al. 1987). Therefore, one purpose of leaving a refuge is to seek exposure to heat, either directly from solar radiation or indirectly from warm air (Martín and López 1999). Thermoregulatory behaviour utilized by lizards includes movement between sun and shade, or between hot and cold environments (Huey and Slatkin 1976 and references therein). An increased body temperature will increase sprint speed, foraging success, and capacity to escape predation (Verwaijen and Van Damme 2007 and references therein). In areas with a cool climate, the activities of lizards are therefore restricted to a certain period of the year, as well as certain hours of the day (e.g., Burke and Ner 2005).

The northernmost reptile, the Common Lizard (*Zootoca* (*Lacerta*) *vivipara* (Jacquin, 1787)), occurs over most of the Palearctic region northwards to the Arctic Sea, and inhabits open habitats such as peat bogs and heath lands (Pilorge 1987; Strijbosch 1988; Lorenzon et al. 1999; Grenot et al. 2000). Its activity pattern is strongly dependent on the prevailing weather conditions, and in particular the amount of solar radiation (Van Damme et al. 1987 and references therein). Furthermore, individuals from northern Sweden (67°N) were found to have higher endurance at lower temperature than individuals from southern Sweden (57°N; Uller and Olsson 2003). Common Lizards respond to long-lasting cloudy weather by retreating underground but resume activity quickly when direct sunlight is accessible (Van Damme et al. 1987). By being dependent on high ambient temperatures for their activity, and thus being more active on warmer days, lizards may suffer weather-dependent predation risk (Huey and Slatkin 1976). In particular, by basking, and especially by being more active after having obtained a higher body temperature, lizards are probably more visible to avian predators on sunny days and the warmest periods of the day. However, there is very limited data on how raptors respond to changes in prey availability associated with ambient temperature and time of day (for an exception see Stinson 1980).

An important avian predator on the Common Lizard is the Eurasian Kestrel (*Falco tinnunculus* L., 1758), hereafter called the kestrel, an open country raptor that takes mainly ground-dwelling prey such as voles (Cricetidae), shrews (Soricidae), birds, lizards, and insects (Village 1990). In this study, we tested whether the kestrel more often prey upon Common Lizards at low temperatures, such as early in the morning or late in the evening, when the lizards can attain optimal body temperature only by basking in open habitats (cf. Van Damme et al. 1987 and references therein), or, alternatively, during spells of high temperatures and during midday periods when solar radiation is strongest, when the lizards are more active, shuttling between sun and shade, foraging, and mating (Lorenzon et al. 1999). We obtained data for this test by video monitoring of prey deliveries to kestrel nests. To circumvent the problem that no delivery of lizards could either mean that the kestrels foraged on other prey types or simply that the kestrels were not foraging at all, we controlled for any diel variation in the foraging activity of the kestrels by using the probability of a prey item delivered being a lizard as the response variable, and not the delivery rate of lizards per se.

Materials and methods

Study area and video monitoring

The study was conducted in an area of approximately 2000 km^2 in the boreal zones in Hedmark county in southeastern Norway (61°N, 12°E) during June and July in 2003 and 2005–2009. Here male kestrels providing for their family prefer to hunt in peat bogs with sparse trees (Løken 2009). This habitat is also favoured by the Common Lizard (Strijbosch 1988), which is the only lizard species occurring in the study area. The climate is relatively cool, so the lizards need to invest much time in thermoregulation for maintaining an optimal body temperature (cf. Herczeg et al. 2008). Mean daily ambient temperature when recording prey deliveries was 15 °C (range –1 to 31 °C for the four daily records, see below). At summer solstice, sunrise and sunset is at 0331 and 2255 local summer time (GMT + 2 h), respectively, in the study area.

The frequency of lizards among prey delivered by kestrels was estimated by video monitoring of prey deliveries to nest boxes used by kestrels for breeding. The nest boxes were mounted in solitary trees located in clear-cuts and heath bogs, surrounded by coniferous forest with only negligible patches of agricultural land. We had access to >100 kestrel nests each year and mounted cameras in a total of 55 nests; 9 nests in 2003, 10 nests in 2005, 6 nests in 2006, 10 nests in 2007, 11 nests in 2008, and 9 nests in 2009. Each nest was filmed for 2 days in 2003, 2005, and 2006, for approximately 14 days in 2007, and for 3 days in 2008 and 2009. The filming days represent a wide range of brood ages from 8 to 29 days. Each filming day lasted approximately 11 h (approximately 0600–1700) in 2003, approximately 10 h (0600–1600) in 2005, and approximately 11 h (approximately 0600–0900 to 1800–2100) in 2006. In 2007–2009, the nests were filmed continuously throughout the whole day and night. For each nest, except the ones filmed in 2003, the original nest box was replaced with a new box designed to accommodate video monitoring. In 2003, a mini-DV camcorder was used for monitoring the kestrels. In 2005, an external camera was used in combination with a mini-DV camcorder as a recording unit. In 2006, both an external camera and a mini-DV camcorder were used in combination with a time-lapse video recorder (VHS) and a hard-disk recorder (HDD). In 2007–2009, we used a mini digital video recorder in combination with an external camera (for details see Steen 2009). Different setups between years were a consequence of technical improvement, i.e., more efficient installation procedure and easier maintenance. All setups were equally capable of recognizing prey items delivered at the nests.

Prey delivery and meteorological data

We identified each prey item delivered by the kestrels to type, i.e., whether it was a lizard, a shrew, a vole, or a bird, or, very rarely, a frog or an insect. In a few cases, the parent landed on the nest box with a prey item without providing it to the nestlings. Instead, the parent departed with the prey item and later returned with the seemingly same prey item, which sometimes was more prepared (e.g., removed head, feathers, or intestines). To avoid duplicate counting of prey items, we counted only one delivery when the time between departure and return was 30 min or less in such cases (n = 47).

The 55 nests monitored were in 47 different nest boxes; i.e., 6 nest boxes were filmed for 2 years and 1 nest box for 3 years. Of the nest boxes filmed for 2 years, three were filmed in subsequent years, one was filmed 3 years apart, and two were filmed 5 years apart. The nest box filmed for 3 years was first filmed 2 years apart and then 3 years apart. In our study area, the kestrel is a migrant that arrives in April and May. Also in western Finland (63°N), the kestrel is a migrant; only 25% of the males and 8% of the females reuse the same nest site in successive years (Tolonen and Korpimäki 1995). In Scotland (55°N), where the kestrel is partly resident, 29% of males and 18% of females reuse the same nest site in successive years (Village 1990). Applying these high turnover rates on our reuse of boxes for filming suggests that one individual or less of each sex would have been filmed at two nests. Thus, we assume that very few, if any, adult kestrel was involved in more than one of our 55 monitoring sessions. Therefore, we treated breeding pairs as the statistical unit.

To examine the effect of external heat on the probability that a prey item delivered by the kestrels was a lizard, we used the ambient temperature at the time each prey item was delivered at the kestrel nests. The data on ambient temperatures were obtained from the Trysil Vegstasjon official meteorological station, situated central in our study area (61°29′N, 12°27′E; at 360 m elevation), and 16.5 ± 1.0 km (range 3.1–28.8 km) from the nest boxes that we filmed (n = 47). Here, ambient temperature is recorded four times per day (0100, 0700, 1300, and 1900 local summer time; GMT + 2 h). Based on these records, ambient temperature at the time of prey delivery was estimated by linear interpolation. To examine the effect of solar radiation on the probability that an item delivered was a lizard, we used a linear proxy for the solar height, namely the number of hours from solar midnight (0113 local summer time during our study) at the time each prey item was delivered at the kestrel nests, thus a variable taking any value between 0 and 12 h.

Statistical analyses

Statistical analyses were performed with R version 2.8.1 (R Development Core Team 2008), using logistic multilevel regression. The response variable was whether a prey item delivered by the kestrel was a lizard or not (frequency). Explanatory variables were ambient temperature at the time the prey item was delivered, the number of hours from solar midnight, and the interaction term. The variables breeding pair and year were included as random effects (Pinheiro and Bates 2000) to control for any individual differences in the frequency of lizards among prey items delivered, for instance owing to differences in prey abundance between territories or years. Different combinations of the variables in the global model were tested, where the model with the lowest Akaike's information criterion (AIC) value was selected. We kept to the most parsimonious model if ΔAIC was <2.0 after adding a variable (Burnham 2002). We used log-likelihood ratio tests to check for the significance of random effects. We compared the two fitted models with different specifications of the random effects and checked whether removal of a random effect caused a significant decrease in the log-likelihood ratio (Bolker et al. 2009). Breeding pair was kept as a random effect in the model regardless of its significance value to control for possible variation caused by individual differences. Year as a random effect was included in the final model only when being significant at $\alpha = 0.10$.

To control for the possibility that an increase in the probability of a prey item delivered being a lizard was caused by lizards being captured as an alternative when other prey types were less available, we also calculated separate time-specific mean delivery rates of lizards and other prey types. Figures were constructed using SigmaPlot version 9.01 (SPSS Inc., Chicago, Illinois, USA).

Results

A total of 313 lizards were recorded delivered at the nests and provisioned to nestlings by the kestrels, constituting 5.7% of the total number of prey items recorded (n = 5499). The probability that a prey item delivered was a lizard increased significantly with increasing ambient temperature and with number of hours from solar midnight, with no significant interaction effect (Table 1, Fig. 1). The random effect of "year" did not contribute significantly to the model. However, "breeding pair" had a significant random effect and was kept in the model (log-likelihood ratio test: $\chi^2_{[1]} = 83.37$, $p < 0.001$).

The lizards were delivered when ambient temperature was 20.2 ± 0.24 °C (mean ± SE) (n = 313), compared with 15.7 ± 0.05 °C (n = 5186) for the other prey types. The lowest ambient temperature when a lizard was recorded delivered was 7.1 °C and the highest was 31.4 °C. The lizards were delivered between 0642 and 2148. The majority of them were delivered between 1000 and 1700, when the mean ambient temperature at the time of delivery ranged 19.1–22.0 °C (Fig. 2*a*). In comparison, prey items of other types were delivered between 0248 and 2339 (Fig. 2*b*). The delivery rate of these other prey types did not vary between 0700 and 2000 (Fig. 2*b*). Hence, the higher probability of a prey item delivered being a lizard at high ambient temperature and around midday was not an artefact of decreased

Table 1. Parameter estimates from a logistic multilevel regression model with the frequency of Common Lizards (*Zootoca* (*Lacerta*) *vivipara*) among prey delivered to nests of Eurasian Kestrels (*Falco tinnunculus*) as a response variable (n = 5499), and ambient temperature (°C) and hours from solar midnight (0113 local summer time) as explanatory variables.

Explanatory variable	Estimate ± SE	z	p
(Intercept)	–7.72±0.46	–16.61	<0.001
Ambient temperature	0.18±0.02	8.71	<0.001
Hours from solar midnight	0.19±0.03	5.72	<0.001

Note: The estimates are corrected for the random effect of breeding-pair identity (n = 55).

Fig. 1. The probability that a prey item delivered to nests of Eurasian Kestrels (*Falco tinnunculus*) was a Common Lizard (*Zootoca* (*Lacerta*) *vivipara*) as a function of ambient temperature and hours from solar midnight, with the plane describing the complete logistic regression model (calculated from the parameter estimates). Note that the scale on the axis denoting hours from solar midnight (0113 local summer time) is an approximate measure of solar height.

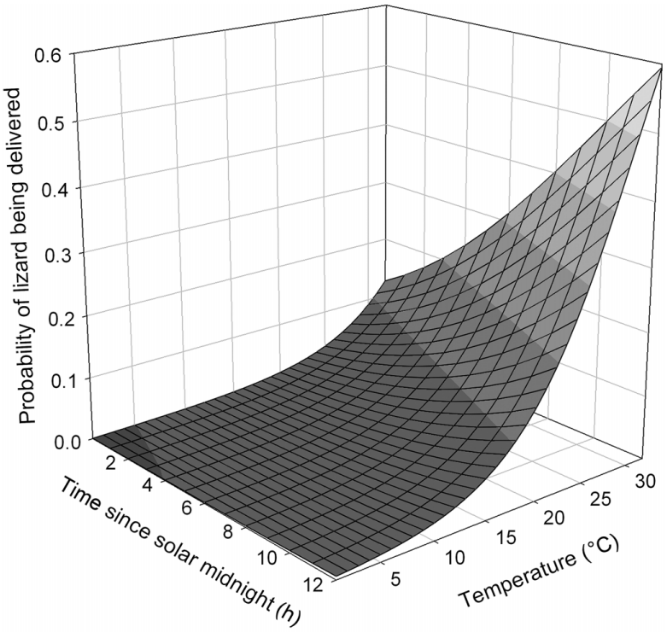
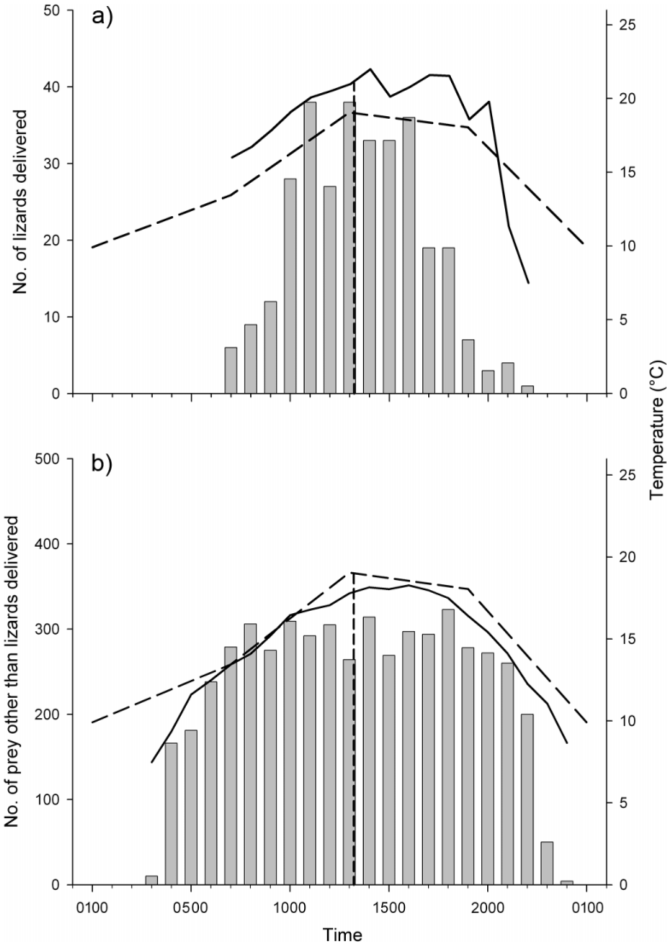


Fig. 2. Number of prey items delivered to nests of Eurasian Kestrels (*Falco tinnunculus*) during each hour of the day (bars; left axis), mean ambient temperature at the time of prey delivery (solid line; right axis), and mean ambient temperature during each hour of the day in the study period (broken line; right axis) based on mean values from the raw data. The vertical broken line denotes midday (1313). (*a*) Common Lizards, *Zootoca* (*Lacerta*) *vivipara* (n = 313). (*b*) Other prey items (insects, amphibians, mammals, and birds; n = 5186).



availability and thus delivery rate of other prey types under these conditions.

Discussion

The probability that a prey item being delivered at kestrel nests was a lizard independently increased with both increasing ambient temperature and proximity to midday compared with earlier and later in the day. Although the delivery rate of prey items other than lizards was quite constant throughout the day, the delivery rate of lizards peaked around midday. This corresponds with the fact that ambient temperature, on average, was 20.2 °C and 15.7 °C, respectively, when lizards and prey items of other types were delivered. The activity level of lizards is known to vary with hydrological conditions and ambient temperatures (Lorenzon et al. 1999). Furthermore, the aerobic metabolic capacity of lizards, which alone is sufficient to supply the required energy for foraging, increases with increasing ambient temperatures in the range of 20–30 °C (Al-Sadoon 1987). Hence, lizards may spend more time foraging at high temperatures, and then be more vulnerable to predation by kestrels because they are more detectable. Also, the activity pattern of the lizard is known to depend strongly on the prevailing weather conditions, in particular on solar radiation (Van Damme et al. 1987 and references therein).

Common Lizards are smaller than the other prey types (except insects) taken by kestrels in our study area; estimated mean body mass of prey delivered at our kestrel nests were 5.3 g for lizards, 9.6 g for shrews, 20.3 g for voles, and 37.8 g for birds (Steen et al. 2010). The size distribution of prey items delivered at a raptor's nest may be a biased estimate of the size distribution of prey items captured by the raptor, because allocation of prey for transport to the nest among those captured may not be random. In fact, raptors in general tend to carry larger prey to the nest and consume smaller prey at the capture site (the ‘‘load-size effect’’; Sonerud 1992 and references therein). The kestrel in particular has been found to consume a higher proportion of Common Lizards at the capture site compared with larger prey (Sonerud 1989). Thus, the proportion of lizards among prey items captured by the kestrels in our study was most likely higher than the proportion of lizards among prey items delivered. Moreover, according to the models presented by Sonerud (1992), the magnitude of this underestimation would depend on the proportion of lizards among prey items captured as explained in the following.

Corrected for prey items allocated for self-feeding, the delivery of lizards by kestrels in our study would reflect their capture of lizards, which may therefore be regarded as a functional response, where the availability of lizards is determined by solar height and ambient temperature (cf. Fig. 2*a* in Sonerud 1992, with lizards as the primary prey and the other and larger prey types as alternative prey). As long as lizard capture rate, as a proportion of total capture rate, is below a threshold, such as at low solar height and low ambient temperature in our study, all lizards captured would be consumed at the capture site and none would be delivered at the nest (cf. Fig. 2*b* in Sonerud 1992). Above this threshold, where more lizards are taken than is needed by the hunting kestrel to fulfil its own energy requirement, lizards would make up an increasing frequency of prey delivered. Thus, our estimate of the proportion of lizards among prey taken by kestrels, based on the sample of prey item delivered at the nest, would be less biased as the capture rate of lizards relative to other prey increases. If we had been able to record all prey items captured by our kestrels, and not only those delivered at the nest, we would have been able to estimate the real functional response curve for the predation of kestrels on lizards. This curve would have laid above the recorded one for all values of ambient temperature and time from midnight, but more so for the lowest values and least for the highest values. Factors other than the load-size effect may influence the allocation of captured prey for consumption at the capture site or transport to the nest, decreasing the difference between the real functional response curve and the one estimated from prey deliveries at the nest (Sonerud 1992; Korpimäki et al. 1994).

The proportion of lizards among prey items delivered to kestrel nests was smaller in our study than in studies made farther south (e.g., Carrillo et al. 1994; Vanzyl 1994; Padilla et al. 2007). This fits a general trend of decreasing occurrence of lizards in the diet of kestrels with increasing latitude (Village 1990), which probably is due to a corresponding decline in lizard abundance with colder climate. Even though lizards apparently contribute little to the breeding success of kestrels in our study area as judged from the frequency of delivery to the nest, they may be important for the providing male owing to the load-size effect. Whereas lizards made up only 14% of prey items carried to the nest by a male kestrel, they made up 64% of vertebrate items consumed at the capture site (Sonerud 1989).

Our finding that lizards were more often delivered by the kestrels as the ambient temperature increased is consistent with that of a study of predation behaviour in Loggerhead Shrikes (*Lanius ludovicianus* L., 1766), where ambient temperature was assumed to be the main determinant of the attack rate on ectothermic prey through its effect on prey activity and thus exposure to predation (Craig 1978). Similarly, at one nest of the Red-tailed Hawk (*Buteo jamaicensis* (J.F. Gmelin, 1788)), where the majority of prey were ectothermic snakes, the probability that a prey item was delivered increased with increasing ambient temperature (Stinson 1980). Our finding that lizards were more often delivered by kestrels around midday independently of ambient temperature contradicts the prediction that kestrels prey upon Common Lizards early in the morning or late in the evening, when the lizards probably are particularly vulnerable because they move slower and can attain optimal body temperature only by basking in open habitats and thus be more exposed (cf. Van Damme et al. 1987 and references therein). To the contrary, our findings support the prediction that kestrels prey upon Common Lizards during spells of high temperatures and at the time of day with the highest solar radiation near midday, when the lizards are more active, shuttling between sun and shade (Lorenzon et al. 1999). However, because we did not collect data on the activity level of the lizards during our study, we are unable to distinguish whether the peak in predation on lizards by kestrels at high solar radiation and ambient temperature is just due to a change in activity rate of the lizard, i.e., numbers of lizards active, or to changes in the vulnerability of lizards through changes in exposure and habitat use.

The probability that a prey item delivered at a kestrel nest was a lizard varied between breeding pairs. This may be due to differences in prey abundance and habitat composition between territories (cf. Costantini et al. 2005) or to individual differences in prey selection behavior. Some individuals may have been hunting in areas where lizards were absent or very few, or they may have specialized on certain prey types. Consistent individual differences, so called behavioral syndromes or animal personalities, have been documented in a variety of animals, including birds (Garamszegi et al. 2009; Kontiainen et al. 2009).

Given that the availability of lizards to kestrels was determined by solar height and ambient temperature, we would assume that during sunny and warm weather, the kestrels would switch foraging tactic to focus on lizards or to restrict their search effort to microhabitats where lizards are most abundant (cf. Holling 1966). As a consequence of an increased presence of the kestrel, the lizards may need to increase their use of refuges and thus alter their thermoregulatory behaviour (cf. Martín and López 1999). Hence, for the lizard, the benefit of obtaining optimal body temperature for maximizing physiological functions by exposure to external heat need to be traded against the increased risk of being preyed upon by the kestrel. However, to tease out the relative contributions of kestrel foraging behavior, lizard availability, and lizard vulnerability to the recorded pattern of increased delivery of lizards with increased solar height and ambient temperature, an integrated study of kestrel and lizard behavior would be needed.

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References

Al-Sadoon, M.K. 1987. The influence of temperature and activity on aerobic and anaerobic metabolism in the viviparous lizard, *Lacerta vivipara* (Jacquin). Herpetol. J. **1**(5): 181–185.

Avery, R.A., Mueller, C.F., Smith, J.A., and Bond, D.J. 1987. The movement patterns of lacertid lizards: speed, gait and pauses in *Lacerta vivipara*. J. Zool. (Lond.), **211**(1): 47–63. doi:10.1111/j.1469-7998.1987.tb07452.x.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., and White, J.S.S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. **24**(3): 127–135. doi:10.1016/j.tree.2008.10.008. PMID:19185386.

Burke, R.L., and Ner, S.E. 2005. Seasonal and diel activity patterns of Italian wall lizards, *Podarcis sicula campestris*, in New York. Northeast. Nat. **12**(3): 349–360. doi:10.1656/1092-6194(2005)012[0349:SADAPO]2.0.CO;2.

Burnham, K.P. 2002. Model selection and multimodel inference: a practical information–theoretic approach. 2nd ed. Springer-Verlag, New York.

Carrillo, J., Hernández, E.C., Nogales, M., Delgado, G., García, R., and Ramos, T. 1994. Geographic variation in the spring diet of *Falco tinnunculus* L. on the islands of Fuerteventura and El-Hierro (Canary Islands). Bonn. Zool. Beitr. **45**(1): 39–48.

Caro, T. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago.

Costantini, D., Casagrande, S., Di Lieto, D., Fanfani, A., and Dell'Omo, G. 2005. Consistent differences in feeding habits between neighbouring breeding kestrels. Behaviour, **142**(9–10): 1409–1421.

Craig, R.B. 1978. An analysis of the predatory behavior of the loggerhead shrike. Auk, **95**(2): 221–234.

Garamszegi, L.Z., Eens, M., and Török, J. 2009. Behavioural syndromes and trappability in free-living collared flycatchers, *Ficedula albicollis*. Anim. Behav. **77**(4): 803–812. doi:10.1016/j.anbehav.2008.12.012.

GilDelgado, J.A., Verdejo, J., and Barba, E. 1995. Nestling diet and fledgling production of Eurasian kestrels (*Falco tinnunculus*) in eastern Spain. J. Raptor Res. **29**(4): 240–244.

Grenot, C.J., Garcin, L., Dao, J., Herold, J.P., Fahys, B., and Tsere-Pages, H. 2000. How does the European common lizard, *Lacerta vivipara*, survive the cold of winter? Comp. Biochem. Physiol. A Mol. Integr. Physiol. **127**(1): 71–80. doi:10.1016/S1095-6433(00)00236-1.

Grønnesby, S., and Nygård, T. 2000. Using time-lapse video monitoring to study prey selection by breeding goshawks *Accipiter gentilis* in Central Norway. Ornis Fenn. **77**(3): 117–129.

Herczeg, G., Herrero, A., Saarikivi, J., Gonda, A., Jäntti, M., and Merilä, J. 2008. Experimental support for the cost–benefit model of lizard thermoregulation: the effects of predation risk and food supply. Oecologia (Berl.), **155**(1): 1–10. doi:10.1007/s00442-007-0886-9.

Holling, C.S. 1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. **48**: 1–86.

Huey, R.B., and Slatkin, M. 1976. Cost and benefits of lizard thermoregulation. Q. Rev. Biol. **51**(3): 363–384. doi:10.1086/409470. PMID:981504.

Kontiainen, P., Pietiainen, H., Huttunen, K., Karell, P., Kolunen, H., and Brommer, J.E. 2009. Aggressive Ural owl mothers recruit more offspring. Behav. Ecol. **20**(4): 789–796. doi:10.1093/beheco/arp062.

Korpimäki, E. 1988. Diet of breeding Tengmalm's owls *Aegolius funereus*: long-term changes and year-to-year variation under cyclic food conditions. Ornis Fenn. **65**(1): 21–30.

Korpimäki, E., Tolonen, P., and Valkama, J. 1994. Functional responses and load-size effect in central place foragers: data from the kestrel and some general comments. Oikos, **69**(3): 504–510. doi:10.2307/3545862.

Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**(4): 619–640. doi:10.1139/z90-092.

Løken, Ø. 2009. Home range, habitat selection and behaviour of male kestrels (*Falco tinnunculus*) in boreal forest. M.Sc. thesis, Norwegian University of Life Sciences, Ås.

Lorenzon, P., Clobert, J., Oppliger, A., and John-Alder, H. 1999. Effect of water constraint on growth rate, activity and body temperature of yearling common lizard (*Lacerta vivipara*). Oecologia (Berl.), **118**(4): 423–430. doi:10.1007/s004420050744.

Machmer, M.M., and Ydenberg, R.C. 1990. Weather and osprey foraging energetics. Can. J. Zool. **68**(1): 40–43. doi:10.1139/z90-007.

Martín, J., and López, P. 1999. When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. Behav. Ecol. **10**(5): 487–492. doi:10.1093/beheco/10.5.487.

Millon, A., Nielsen, J.T., Bretagnolle, V., and Møller, A.P. 2009. Predator–prey relationships in a changing environment: the case of the sparrowhawk and its avian prey community in a rural area. J. Anim. Ecol. **78**(5): 1086–1095. doi:10.1111/j.1365-2656.2009.01575.x. PMID:19558613.

Newton, I. 1979. Population ecology of raptors. T. and A.D. Poyser, Berkhamsted, UK.

Newton, I. 1986. The sparrowhawk. T. and A.D. Poyser, Calton, UK.

Padilla, D.P., Nogales, M., and Marrero, P. 2007. Prey size selection of insular lizards by two sympatric predatory bird species. Acta Ornithol. **42**(2): 167–172.

Pilorge, T. 1987. Density, size structure, and reproductive characteristics of three populations of *Lacerta vivipara* (Sauria, Lacertidae). Herpetologica, **43**(3): 345–356.

Pinheiro, J.C., and Bates, D.M. 2000. Mixed-effects models in S and S-PLUS. Springer-Verlag, New York.

R Development Core Team. 2008. R: a language and environment for statistical computing. Version 2.8.1 [computer program]. R Foundation for Statistical Computing, Vienna, Austria.

Redpath, S.M. 1992. Behavioural interaction between hen harriers and their moorland prey. Ornis Scand. **23**(1): 73–80. doi:10.2307/3676429.

Reif, V., Tornberg, R., Jungell, S., and Korpimäki, E. 2001. Diet variation of common buzzards in Finland supports the alternative prey hypothesis. Ecography, **24**(3): 267–274.

Selås, V. 2001. Predation on reptiles and birds by the common buzzard, *Buteo buteo*, in relation to changes in its main prey. Can. J. Zool. **79**(11): 2086–2093. doi:10.1139/cjz-79-11-2086.

Selås, V., Tveiten, R., and Aanonsen, O.M. 2007. Diet of common buzzards (*Buteo buteo*) in southern Norway determined from prey remains and video recordings. Ornis Fenn. **84**(3): 97–104.

Sonerud, G.A. 1986. Effect of snow cover on seasonal changes in diet, habitat, and regional distribution of raptors that prey on small mammals in boreal zones of Fennoscandia. Holarct. Ecol. **9**(1): 33–47.

Sonerud, G.A. 1989. Allocation of prey between self-consumption and transport in two different-sized central place foragers. Ornis Scand. **20**(1): 69–71. doi:10.2307/3676711.

Sonerud, G.A. 1992. Functional responses of birds of prey: biases due to the load-size effect in central place foragers. Oikos, **63**(2): 223–232. doi:10.2307/3545382.

Steen, R. 2009. A portable digital video surveillance system to monitor prey deliveries at raptor nests. J. Raptor Res. **43**(1): 69–74. doi:10.3356/JRR-08-19.1.

Steen, R., Løw, L.M., Sonerud, G.A., Selås, V., and Slagsvold, T. 2010. The feeding constraint hypothesis: prey preparation as function of nestling age and prey mass in the Eurasian kestrel. Anim. Behav. **80**(1): 147–153. doi:10.1016/j.anbehav.2010.04.015.

Stinson, C.H. 1980. Weather-dependent foraging success and sibling aggression in Red-tailed Hawks in central Washington. Condor, **82**(1): 76–80. doi:10.2307/1366788.

Strijbosch, H. 1988. Habitat selection of *Lacerta vivipara* in a lowland environment. Herpetol. J. **1**(6): 207–210.

Sulkava, S. 1964. Zur Nahrungsbiologia des Habichts, *Accipiter gentilis* (L.). Aquilo Ser. Zool. **3**: 1–103.

Suomus, H. 1952. Studies on the feeding habits of the common buzzard. Riistat. Julk. **8**: 121–127.

Tolonen, P., and Korpimäki, E. 1995. Parental effort of kestrels (*Falco tinnunculus*) in nest defence: effects of laying time, brood size, and varying survival prospects of offspring. Behav. Ecol. **6**(4): 435–441. doi:10.1093/beheco/6.4.435.

Tornberg, R., and Reif, V. 2007. Assessing the diet of birds of prey: a comparison of prey items found in nests and images. Ornis Fenn. **84**(1): 21–31.

Uller, T., and Olsson, M. 2003. Life in the land of the midnight sun: are northern lizards adapted to longer days? Oikos, **101**(2): 317–322. doi:10.1034/j.1600-0706.2003.12374.x.

Van Damme, R., Bauwens, D., and Verheyen, R.F. 1987. Thermoregulatory responses to environmental seasonality by the lizard *Lacerta vivipara*. Herpetologica, **43**(4): 405–415.

Vanzyl, A.J. 1994. Comparison of the diet of the common kestrel *Falco tinnunculus* in South Africa and Europe. Bird Study, **41**: 124–130.

Verwaijen, D., and Van Damme, R. 2007. Correlated evolution of thermal characteristics and foraging strategy in lacertid lizards. J. Therm. Biol. **32**(7–8): 388–395. doi:10.1016/j.jtherbio.2007.05.005.

Village, A. 1990. The kestrel. T. and A.D. Poyser, London.